Relationships between hummingbirds and flowers in the Andes of Colombia

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Synopsis

An account is given of the feeding ecology of hummingbirds in the Eastern Andes of Colombia, based on nine weeks of field work in 1978. Three hummingbird communities were studied, two in the temperate and one in the subtropical zone. The 25 species of hummingbirds observed showed very different degrees of specialization for exploiting the nectar of particular kinds of flowers, from an extreme in *Ensifera,* which appears to have coevolved with and to be dependent on species of *Passiflora,* to generalists which share their nectar sources with other hummingbirds and insects. In the light of these observations we discuss the 'syndrome of ornithophily', the alternative foraging strategies of trap-lining and territoriality, nectar characteristics, and the evolution of ornithophily in the Andean flora.

Introduction

The ecology of hummingbirds has been the subject of much research in the last ten years, with the emphasis on three related aspects: energetics, the structure of local hummingbird guilds (with which may be included flower-piercers and other nectarivores), and coevolutionary relationships between hummingbirds and their food plants. Undoubtedly a prime reason for the popularity of hummingbirds for this kind of research is the fact that under favourable conditions, in the field, quantitative assessments can be made both of their expenditure of energy, of the availability of nectar from different plants, and of the birds' efficiency in obtaining nectar. As a result, tremendous advances have been made in our understanding of the biology of hummingbirds. Stiles (1980) gives a review, with key references.

In comparison with the energetic aspects of hummingbird ecology and with studies of interactions between guild members, coevolutionary relationships have tended to take a subordinate place, a notable exception being the analysis by Stiles (1975) of the relationship between hermit hummingbirds and *Heliconia* species in a lowland forest in Costa Rica. Most field studies have been carried out at high altitudes in Central America, where a relatively small number of hummingbird species coexist. Nothing has been published so far on relationships between hummingbirds and their food plants in what may be called the core area of hummingbird evolution, the subtropical and temperate forests of the Andes from Colombia to Peru, where the greatest number and variety of hummingbird genera and species coexist. It was for this reason that we attempted a survey of the feeding ecology of hummingbirds in the Eastern Andes of Colombia in July and August 1978, the results of which are presented in this paper.

It must be stressed at the outset that our findings represent the merest scratching at the surface of a subject of great complexity. Our observations extended over only two months, with a span of only three weeks in each of the three areas (two forest, one farmland) in which we worked; but even in that time in all three areas there were significant changes in the availability of nectar, as some plants finished and new ones came into flower. In any area, field work must obviously be continued over at least a complete year in order to get an adequate idea of the food resources available to hummingbirds. In addition, the vegetation was almost entirely different in the two forest areas, about 150 km apart, and the hummingbird species were largely different. Many areas would have to be sampled in order to get an adequate idea

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of the overall distributional pattern of vegetational communities and their associated hummingbirds, even in a small section of the Andes.

Recent research on hummingbird ecology has revealed an important distinction between two fundamentally different feeding strategies. A hummingbird may defend a feeding territory, usually a concentrated source of nectar of small extent such as a single profusely flowering tree, or it may make the rounds of many scattered sources of nectar which it does not attempt to defend, a strategy generally known as 'trap-lining'. Territorial hummingbirds are usually unspecialized feeders, not closely adapted to feeding at particular kinds of flower; trap-lining hummingbirds are typically specialists, adapted to visiting a few kinds of flowers. This division of feeding strategies will be discussed later with reference to our observations in the Andes; we mention it here as we refer to trap-lining and territorial feeding in the species accounts that precede the discussion.

Study areas

Our original intention was to spend the whole of our time in one area, on the eastern slopes of the Eastern Andes, quite close to Bogotá. Owing to unforeseen circumstances we were forced to leave this area half way through the period, and moved to another locality about 150 km to the NNE, on the western slopes of the Eastern Andes, where observations were made in two areas several kilometres apart. The three study areas (referred to in what follows as Fonté, Carare and Togui) are briefly described below. The first two are in the lower part of the Temperate Zone, as defined by Meyer de Schauensee (1964), and the third is near the lower limit of the Subtropical Zone.

Slopes of Cerro Fonté, Vereda de Ferralarada, Municipio de Choachí, Cundina-marca (4° 32′ N, 73° 51′ W), 2400–2550 m; 3–25 July. Gently sloping, western-facing mountainsides, partly wooded, partly cleared for primitive agriculture (pasture, small fields of potatoes and maize), cleared areas in places reverting to bushy secondary growth. Woods mostly with trees not over 15 m in height (perhaps secondary, resulting from earlier clearances).

Slopes of Cerro Carare, 9 km ESE of Togui, Mun. Togui, Boyacá (5° 54′ N, 73° 25′ W), 2300–2500 m; 29 July–3 August, 14–22 August. Natural forest on gentle or moderate slopes, thinned in places by extraction of larger trees, with open areas (some cleared for farming, some probably naturally unforested, due to poor drainage).

Hacienda Versalles, near Togui, Boyacá (5° 55′ N, 73° 32′ W), 1700 m; 27–30 July, 4–14 and 23–24 August. Cattle farm with sugar cane, maize and 3 small patches of coffee, natural vegetation almost entirely gone; trees confined to strips along river banks and between fields; *Eugenia jambos* (introduced) more abundant than any other tree.

Methods

A special effort was made to find all the flowers that were being fed at by hummingbirds in each area at the time of our visits. Flowers were measured (internal length of tubular part of corolla, from opening to base), and measurements were made of nectar concentrations and rates of nectar production. Nectar was extracted with disposable micropipettes (manu-factured by Camlab, Cambridge, England) of various capacities (5 to 100 µl), and sugar concentrations were measured with a Bellingham & Stanley pocket refractometer calibrated from 0 to 50%. Percentage concentrations were not compensated for temperature, but at the temperatures and concentrations recorded compensations are all below 0·4% and thus negligible. To measure nectar production rates, flowers were drained of nectar and then bagged, so as to be inaccessible to birds over the period of the measurement.

Observations of the feeding behaviour of hummingbirds were made with 8× and 10× binoculars, usually at fairly close quarters. Some observations were 'casual', i.e. made during

random walks in the area, during which all observed feeding was recorded; but most were made during timed watches at nectar sources which we had found to be, or suspected to be, important. Each visit by an individual hummingbird to one plant or (in the case of some herbaceous plants, small bushes and clumped trees) group of plants was counted as a unit for purposes of tabulation. When practicable, stop-watch timings were made of the rate at which flowers were visited, and the number and duration of probes into individual flowers.

A limited number of hummingbirds were caught in mist-nets, weighed, measured, and marked with quick-drying paint (dope), mainly on the central tail-feathers, or with coloured inks on white or pale parts of the plumage, for future identification in the field.

Specimens of food plants were collected, and have been deposited in the Herbarium of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia.

The hummingbirds

On the basis of Meyer de Schauensee's (1964) statements of ranges and altitudinal zones of hummingbirds in Colombia, a potential total of 21 species might occur in the Temperate Zone in the vicinity of Carare and Fonté. Five of these were not to be expected in our study areas, as they are birds of open country or of the upper part of the Temperate Zone, above the level where we worked. Of the remaining 16 species, we recorded 14 in one or both of our study areas. The two species not recorded were *Coeligena bonapartei,* which might have occurred at Carare, and *Ramphomicron microrhynchum,* which might have occurred in both areas.

Again on the basis of Meyer de Schauensee's statements, there are 18 species that reach their upper limits in the Subtropical Zone and, from their geographical ranges, might have been expected in at least one of our study areas. Of these, five were recorded in the Carare and/or Fonté study areas, and four more at Togui. Hence our sampling of the more strictly subtropical hummingbirds was much less complete than our sampling of the temperate species, as would be expected from the fact that our two main study areas were at lower temperate levels and the subtropical Togui study area had very little natural vegetation.

All the species recorded are listed, together with weights and measurements, in Table 1.

Observations at Fonté

Vegetation, and available nectar sources

As already mentioned, the woods in the Fonté study area consisted mainly of rather small trees, not over 15 m in height, and may mostly have been secondary, resulting from earlier clearances. Some tracts, consisting almost entirely of one species of Melastomataceae, were certainly secondary. In some places the undergrowth of unfenced woods had been badly damaged by cattle infiltrating from adjacent pastures. In some rocky and steep places the trees were higher and more massive, and the vegetation probably approximated to the natural condition.

Very few of the canopy trees had flowers attractive to hummingbirds at the time of our visit; the only two that were found, *Symplocos mucronata* and an unidentified species, were both uncommon. Epiphytic bromeliads of several species were numerous on the larger trees, but were not in flower at the time of our visit.

The under-storey of the woods in the lower part of the study area consisted largely of slender, straggling trees of a single species, *Palicourea angustifolia,* which were in flower at the time of our visit and were the most important nectar source for the unspecialized hummingbirds. This tree was much less abundant in the upper part of the area, where another, larger species of *Palicourea* was fairly common. This latter species, *P.* cf. *anacardifolia,* had just finished flowering at the time of our visit and most trees had unripe fruit; almost certainly it had been an important nectar source in the period immediately before our arrival. The only other under-storey trees and shrubs seen to be fed at by hummingbirds were: *Symbolanthus tricolor,* a sparsely distributed straggling shrub; *Psychotria* cf. *aschersonianoides,* a small locally common shrub; and *Cinchona* cf.

Table 1 Wing-lengths, bill-lengths and weights of hummingbirds recorded at Fonté (F), Carare (C) and Togui (T)

	Area	Wing mm	Bill (exposed culmen) mm	Bill as % of wing	Weight g
Doryfera ludoviciae	C	60·0	32·9	54·8	5·7
Phaethornis guy	T	61·3	44·3	72·3	5·2
Colibri thalassinus	C	65·6	20·8	31·3	5·3
Colibri coruscans	FC	77·2	24·2	31·3	7·8
Anthracothorax nigricollis	T	65·7	24·8	37·7	7·0
Chlorostilbon gibsoni	T	46·1	16·2	35·1	3·1
Chlorostilbon poortmani	FC	42·5	16·5	38·8	—
Amazilia franciae	T	53·6	24·3	45·2	5·0
Amazilia cyanifrons	T	54·5	17·8	32·6	5·0
Amazilia tzacatl	T	55·0	20·4	37·1	4·8
Adelomyia melanogenys	CT	52·8	15·2	28·8	4·2
Lafresnaya lafresnayi	F	61·7	25·2	40·8	5·9
Coeligena prunellei	C	77·8	29·8	38·3	7·4
Coeligena helianthea	F	71·6	29·9	41·8	—
Coeligena torquata	C	75·5	33·0	43·7	7·0
Ensifera ensifera	F	76·5	83·1[1]	108·6	12·5
Boissoneaua flavescens	C	76·7	17·9	23·3	8·6
Heliangelus amethysticollis	FC	64·3	18·0	28·0	5·9
Eriocnemis vestitus	F	59·3	18·3	30·9	4·9
Eriocnemis cupreoventris	F	61·6	18·6	30·2	5·6
Ocreatus underwoodi	C	43·1	14·0	32·5	3·1
Lesbia nuna	F	50·7	10·0	19·7	—
Metallura tyrianthina	F	53·8	11·0	20·4	3·4
Aglaiocercus kingi	C	53·5	15·2	28·4	4·4
Acestrura mulsant	FCT	40·4	16·7	41·3	3·2

Note: All figures are means. Sexes are combined. Measurements are from museum specimens from the Eastern Andes of Colombia, supplemented by data from this study. Weights are from this study, supplemented by data from Greenewalt (1962), Miller (1963), Carpenter (1976) and Feinsinger *et al.* (1979).

[1] Bill-length very variable, up to c. 105 mm. Effective length for probing tubular flowers is about 10 mm greater than bill-length, owing to marked narrowing of the skull towards the base of the bill.

pitoyensis, a rather uncommon tree in the upper part of the study area. Among the vines, *Pentadenia strigosa* was common in all the woods with undisturbed undergrowth. Its large orange flowers, borne almost from ground level up to about 5 m, were conspicuous in the woody and mossy undergrowth.

Along wood-edges and in more open, rocky areas an ericaceous shrub, *Cavendishia cordifolia,* was locally abundant and in flower. As a nectar source for several hummingbird species it was second only to *Palicourea angustifolia.* Only two other ericaceous plants were found in flower, *Disterigma alaternoides,* which was rare, and a single example of an unidentified species. The poverty of the Ericaceae was in marked contrast to their richness and abundance at Carare (p. 117).

In bushy second growth, especially along edges, several hummingbird flowers were fairly abundant. *Castilleja fissifolia,* a scrambling shrub, was common in such places. *Passiflora mixta,* a vine with very long tubular flowers, was more local but conspicuous where present. An abundant low scrambling shrub, *Siphocampylus bogotensis,* began to come into flower about half way through our visit. *Manettia coccocypseloides,* a climber with small white flowers, was more local. Blackberries, *Rubus* spp., were abundant and in all stages of flower and fruit. *Cuphea dipetala,* a slender shrub, was generally distributed in bushy areas but sparse. *Rubus* and *Cuphea* also grew as low plants out in the open in neglected fields.

Table 2 Characteristics of hummingbird flowers, Fonté

		length of tube (mm)	Corolla colour	orientation[1]	concentration[2] %	Nectar production[3] per hour	per 24 hrs[4]
Theaceae	Symplocos mucronata	10	pink	H	—	—	—
Passifloraceae	Passiflora mixta	114	pink	H	22–30, 25.5	12.0 (max 32.2)	506
Ericaceae	Cavendishia cordifolia	15	pink & white	H–P	9–22, 14.9	1.2 (max 4.0)	22.3
	Disterigma alaternoides	7	white	H	—	—	—
Rosaceae	Rubus sp.	nil	pink & white	H–U	—	—	—
Lythraceae	Cuphea dipetala	18	mauve	H	33	—	—
Tropaeolaceae	Tropaeolum tuberosum	24	orange	H	—	—	—
Gentianaceae	Symbolanthus tricolor	36	pink	H	19	1.5	11.0
Scrophulariaceae	Castilleja fissifolia	19[5]	green (calyx red)	H	16–23, 18.7	—	33.5
Gesneriaceae	Pentadenia strigosa	28	orange	H	24–31, 27.0	—	32.5
Campanulaceae	Siphocampylus bogotensis	55	red	H	21	1.0	—
	Manettia coccocypseloides	12	white	H	—	—	—
Rubiaceae	Palicourea cf. anacardifolia	20	yellow	H	—	—	—
	Palicourea angustifolia	13	mauve	H	10–18, 13.8	1.0 (max 3.9)	29.5
	Psychotria aschersonianoides	6	white	H	—	—	—

Notes: [1] H = horizontal; P = pendent; U = upright.
[2] range and mean. Single figures indicate single measurements.
[3] mean (and maximum recorded)
[4] maximum recorded; for further details, see text.
[5] length of closed tube; see text.

No other plants were important nectar sources at the time of our visit. Over 99% of all hummingbird feeding records were from the plants mentioned above. Flower and nectar characteristics of the majority of them are given in Table 2, and further details of the most important of them are given in the following section.

The most important nectar sources

Palicourea angustifolia

The tubular mauve flowers are borne in racemes. Most racemes did not hold more than 6 open, nectar-producing flowers at a time. Individual flowers lasted 2–3 days. The figures for nectar concentration given in Table 2 are based on 46 out of 50 readings, four very low readings being omitted (5–9%). Concentrations tended to be higher in the early morning (14–18%) than at midday or in the afternoon (10–16%). There was also some decrease in concentration with the age of the flower: the last readings for 6 flowers, immediately before the end of their nectar production, averaged 11% (range 6–13%). Nectar production rates also were highest in the morning, the average for 12 morning rates being 1·23 µl/hr, while rates for the whole day averaged 0·97 µl/hr. Hourly rates for the night (which included the early evening and very early morning) averaged 0·41 µl/hr. The maximum figure for nectar production over 24 hours given in Table 2 (29·5 µl) was approached by two others (28·5, 27·9), while three others were considerably lower (21·5, 13·8, 9·1). Age of the flowers might largely have accounted for these differences.

Because of its abundance, the considerable number of flowering racemes on even quite small plants, and its short corolla tube, *Palicourea angustifolia* offered an abundant nectar supply to the shortest-billed of the hummingbirds, as well as to those with longer bills. Several timings of *Eriocnemis vestitus* showed that it visited *Palicourea* flowers at a rate of one flower every 1·3 s (combined figures, 141 flowers in 178 s), and this rate seemed typical of the smaller hummingbird species. As mentioned later, four species of hummingbirds maintained feeding territories at *Palicourea* clumps.

Cavendishia cordifolia

The tubular, pale pink and white flowers of this heath are borne in terminal clusters, protected by scaly sheaths of pink bracts. Individual flowers last 2–3 days. The figures for nectar concentration given in Table 2 are based on 32 of 36 readings, the four omitted being abnormally low (2–6%). The nectar concentration of individual flowers was rather consistent over 2 or more days (i.e. some had consistently high, and some low concentrations), with a tendency for concentrations to decrease very slightly in the course of a day (by 0·6%, average of 10), and from one day to the next (by 1·5%, average of 6).

As already mentioned, *Cavendishia* was second in importance only to *Palicourea* as a nectar source for several hummingbird species. The richest feeding areas for these birds were along wood-edges, where both *Palicourea* and *Cavendishia* frequently grew side by side.

Castilleja fissifolia

The flowers are borne in terminal spikes, the pale green corolla being ensheathed along most of its length by the calyx whose distal half is red. The corolla is slightly curved along its whole length; it is tubular basally (for the proximal 20 mm), but distally is split along the under-side (for the distal 25 mm). In spite of many attempts, we never found it easy to extract much nectar from *Castilleja* flowers. Recorded nectar concentrations were 23, 17 and 16%. The maximum figure for nectar production over 24 hours was 11 µl; other figures were 8, 6 and 1 µl.

Castilleja was one of the preferred flowers of *Lafresnaya lafresnayi,* whose curved bill fits the corolla exactly. Almost certainly *Lafresnaya* is the plant's chief pollinator, as was indicated by the pale pollen that conspicuously coated their foreheads when they were feeding on

it. The only other hummingbird seen to visit *Castilleja* flowers, *Lesbia nuna,* has a much shorter, straight bill. It either probed the flowers at the base of the split in the corolla, about 19 mm from the nectary, or pierced the base of the calyx, on the upper side. Neither method would bring it into contact with the anthers or stigma.

Passiflora mixta

The long tubular flowers, with a ring of pink petals round the entrance to the tube, arise singly from leaf axils near the growing tip of the long climbing and sprawling stems. Along each stem only one or two flowers are open and producing nectar at any time, those that are distal being in bud and those that are proximal in fruit. Each flower usually lasts 4–5 days (extremes of 3 and 6 recorded). The figures for nectar concentration in Table 2 are based on 19 out of 22 readings, the three omitted being very low (17–18%). Two of the very low readings, and perhaps the third, were from flowers that were nearly over. (A reading of 12% from a flower that was already withered is also omitted). Nectar concentrations remained rather steady throughout the day; but measurements of individual flowers on successive days indicated that concentration rises and then falls during the life of the flower. Nectar production is copious, but also very variable, the maximum amount produced in 24 hours shown in Table 2 (506 µl) being a good deal more than the next highest (397 µl). A younger flower on the same plant as the latter produced only 81 µl on the same day in the same 24-hour period. Another flower produced 98 µl in one 24-hour period, and 150 µl in the next.

Ensifera ensifera is the only hummingbird that we saw taking nectar 'legitimately' from *Passiflora mixta,* i.e. by entering through the opening of the corolla tube, and in fact is the only one that could possibly do so, its effective bill length (Table 1) being almost the same as the *Passiflora* corolla tube. Practically all the *Passiflora* flowers in the study area were, however, pierced at the base by the flower-piercer *Diglossa albilatera,* and hummingbirds of several species extracted nectar from the holes made by *Diglossa.* Consequently, unprotected *Passiflora* flowers usually contained very little nectar. The effect of this nectar 'thieving' on *Ensifera* is discussed later (p. 115).

Pentadenia strigosa

This climbing plant was abundant in shady places, especially among rocky outcrops. It flowered as low as a few cm from the ground in dense second growth and up to 5 m where it had clambered up trees in older woodland. The flowers grow in pairs along the stem, both members of a pair opening at about the same time; they last 7–8 days and are protandrous. The hairy orange corolla is in the form of a wide tube (28 mm long, 18 mm deep), decurved distally and opening downwards, and is borne horizontally, suspended at the end of the long, vertically hanging pedicel.

Only *Lafresnaya* females were seen feeding at *Pentadenia* flowers; no flower-piercers were seen to visit them and no pierce holes were found on the flowers examined. Several features of the flower suggest adaptations protecting the nectar against flower-piercers: the delicate suspension of the flower at the end of the long pedicel, which would make it difficult to perch on and inaccessible from other perches, and the wide, rounded corolla tube, which would be difficult for a flower-piercer to grasp and pierce.

Symbolanthus tricolor

The pink flowers, with darker pink streaks, are borne very sparsely, only 1–4 being open at a time on the few plants that were seen. The nectaries are protected by the tough thick calyx base. Only a single reading of nectar concentration was made, and one measurement of rate of nectar production (Table 2). Two hummingbird species, *Coeligena helianthea* and *Lafresnaya,* were seen visiting these flowers.

Siphocampylus bogotensis

Little information was obtained on this plant, as its flowering season was only just beginning

when we left the area. The nectar concentration and production rates given in Table 2 are based on single measurements. It seemed very likely that *Siphocampylus* was going to be an important nectar source for *Lafresnaya,* the only hummingbird species seen to visit it. The corolla length and curvature fit *Lafresnaya*'s bill closely. The flowers are soft, with no protection of the nectaries, and preliminary observations indicated that *Diglossa albilatera* regularly pierced them at the base.

Feeding ecology of the hummingbirds

Of the 11 species of hummingbirds recorded on Fonté, all but two were regularly present and seen whenever watches were kept at appropriate flowers. The two exceptions were *Acestrura mulsant,* which was seen only once, and *Colibri coruscans,* which was abundant at lower levels (below c.2200 m) but only once seen at the lower edge of our study area. The nine resident species can be divided into three groups: four medium-sized to small woodland species with short, straight bills, which held territories centred on food plants with short corolla tubes *(Heliangelus amethysticollis, Eriocnemis cupreoventris, E. vestitus, Metallura tyrianthina);* three larger, long-billed species of woodland or woodland edge, feeding mainly or entirely on specialized hummingbird flowers and non-territorial *(Lafresnaya lafresnayi, Coeligena helianthea, Ensifera ensifera);* and two small open-country species *(Lesbia nuna, Chlorostilbon poortmani).* The feeding records for these hummingbirds are summarized in Table 3.

Three species of flower-piercers *(Diglossa* spp.) occurred in the study area, two of which exploited hummingbird flowers. One of them, *D. albilatera,* was abundant and had a significant effect on the feeding ecology of the hummingbirds with which it competed for nectar.

Table 3 Hummingbird feeding records, Fonté

	C.p.	L.l.♂	L.l.♀	C.h.	E.e.	H.a.	E.v.	E.c.	L.n.	M.t.
Shrubs and scramblers										
Cavendishia cordifolia	1	1		16		5	11	13	4	3
Rubus sp.				3					6	16
Cuphaea dipetala	1		1					1	7	1
Symbolanthus tricolor			5	6						1[1]
Castilleja fissifolia		1	17						35[1]	
Siphocampylus bogotensis		1	6							1[1]
Psychotria aschersonianoides										6
Vines/climbers										
Passiflora mixta				29[1]	10		1[1]	3[1]		29[1]
Pentadenia strigosa			8							
Manettia coccocypseloides										7
Trees										
Cinchona cf. *pitoyensis*										1
Palicourea cf. *anacardifolia*				1						1
Palicourea angustifolia	1	23	4	5		21	6	12	3	69
Other plants	2	3	1	1						7
Insect-hawking		2	2				1	7	16	5
Totals (453)	5	31	44	61	10	26	19	36	74	147

Hummingbirds abbreviated as follows: *C.h., Coeligena helianthea; C.p., Chlorostilbon poortmani; E.c., Eriocnemis cupreoventris; E.e., Ensifera ensifera; E.v., Eriocnemis vestitus; H.a., Heliangelus amethysticollis; L.l., Lafresnaya lafresnayi; L.n., Lesbia nuna; M.t., Metallura tyrianthina.*

Note: [1] nectar taken 'illegitimately', through hole in corolla base.

Heliangelus amethysticollis
Eriocnemis cupreoventris
Eriocnemis vestitus
Metallura tyrianthina

These four straight-billed, medium-sized to small hummingbirds are treated together, as all fed largely on *Palicourea angustifolia* and (especially *Eriocnemis* spp.) on *Cavendishia cordifolia,* and individuals of all four held feeding territories centred on these plants. They frequently came into conflict with one another, dominance relations being in accordance with their size, i.e. in the order in which they are listed above.

A small wood, measuring about 100 by 30 m (0·3 ha), surrounded on three sides by pasture and on the fourth by scrub, with an under-storey consisting largely of *Palicourea* while *Cavendishia* grew abundantly along the edges, contained an extraordinary number of hummingbirds of these four species for the first two weeks of our visit. Towards the end, the flowering season of *Palicourea* appeared to be coming to an end and the number of hummingbirds decreased. Accurate censusing was not possible in the dense growth within the wood, but probably at least 25 birds were present around the middle of July. Trapping also gave some idea of the numbers. Nine different individuals were caught in two 13-m mist-nets set within the wood on 10–11 July (2 *Heliangelus,* 4 *E. cupreoventris,* 1 *E. vestitus,* 2 *Metallura*), and on 18 July nets set in the same positions caught six different birds (1 *Heliangelus,* 3 *E. cupreoventris,* 2 *Metallura*), all except one *Metallura* different from the individuals caught a week earlier. Several hours were spent in looking for marked birds 2–4 days after the netting operations, but only three marked individuals were seen among the many that were examined. It seemed that individuals were holding very small feeding territories, many of them perhaps rather briefly. There was much trespassing and chases were very frequent, especially early in the period, but were almost always impossible to follow for more than a second or two. Two *Heliangelus* territories (one in an adjacent wood with similar vegetation) consisted of (1) several *Palicourea* bushes spread over a space of 10 by 9 m, and (2) two *Cavendishia* bushes about 10 m apart.

In an even smaller copse, roughly circular and about 25 m in diameter, with sparse *Palicourea* in the under-storey and a few *Cavendishia* bushes round the edge, a single male *E. vestitus* held a territory from 7 to 21 July, effectively excluding other hummingbirds from the area. It also chased intruding White-sided Flower-piercers *Diglossa albilatera,* which were present in all the larger woods, so persistently that it effectively excluded them, thus maintaining its nectar resources intact. On 22 July, when the number of *Palicourea* flowers had declined somewhat, it disappeared and its place was taken almost immediately by a *Metallura,* which occupied the area and patrolled it much as *E. vestitus* had done, but was unable to prevent occasional visits by *Lafresnaya* and *Lesbia nuna.* It seemed that the nectar supply had become insufficient to maintain *E. vestitus* but could still maintain the smaller *Metallura.*

There were some differences in habitat preference between these four hummingbirds. We did not record *Heliangelus* outside more or less closed woodland, whereas *E. cupreoventris* and *Metallura* showed some preference for woodland edges, at times coming well into the open. Rather few observations were made of *E. vestitus,* the least common of the four species (as the trapping figures indicate), but from the records it appeared to favour more open habitats than the others. This is consistent with its general distribution: according to Meyer de Schauensee (1964) it is a bird of the temperate and lower páramo (i.e. more open) zones, whereas *E. cupreoventris* is a bird of the subtropical (more densely wooded) and temperate zones. Among the species that we observed, they were the only examples of overlap between two closely related species with different altitudinal preferences.

Some of the differences between the feeding records for the four species probably resulted from these differences in habitat preference; for instance the marked preponderance of feeding at *Palicourea* by *Heliangelus,* which fed within the woods, compared with the slight preponderance of feeding at *Cavendishia* by the two *Eriocnemis* species, which fed more in the open. The lack of records of *Heliangelus* feeding at *Passiflora* may have the same

explanation. The very few records of feeding at *Cavendishia* by *Metallura,* however, indicate active avoidance of *Cavendishia* flowers, whose 15 mm corolla tubes may be too long for efficient probing by *Metallura*'s 11 mm bill. *Metallura* showed much the greatest variety in its nectar feeding of all the species in the area (Table 3), especially in visiting small flowers not seen to be visited by other species *(Psychotria, Manettia, Symplocos).*

Lafresnaya lafresnayi

This was the only hummingbird with a markedly decurved bill in the Fonté study area. It is, in fact, the only species with such a bill that occurs at temperate levels anywhere in the Andes. Our feeding records for males and females were very different, and so are treated separately. It is probably significant that females, although shorter-winged, have on average longer bills than males. The mean difference in bill-length is only about 2 mm, but a long-billed female may have a bill 4 mm longer than a short-billed male, and such a difference may well affect their relative efficiency in feeding at different flowers.

Females were recorded feeding mainly at flowers of four species whose long corolla tubes fitted their bills rather closely *(Castilleja, Symbolanthus, Pentadenia* and *Siphocampylus).* Three of these were not seen to be visited 'legitimately' by any other hummingbird species and probably depended on *Lafresnaya* for pollination (see also above, under *Castilleja*). In their behaviour, females seemed to be typical trap-liners, reminiscent of hermit hummingbirds *Phaethornis,* moving between scattered nectar sources and showing no tendency to defend a feeding territory. As mentioned later, a female that regularly visited a large *Castilleja* clump at which a female *Lesbia nuna,* a much smaller bird, held a territory was regularly chased by the latter. They fed silently, but during longer flights between nectar sources regularly uttered a monosyllabic 'seep' (reminiscent of the flight call of some *Phaethornis* species).

Watches at places that females visited on their foraging rounds gave some idea of the timing of their feeding routine. Of 17 intervals between successive visits of what was probably the same bird to a nectar source, 15 were from 10 to 31 min, with a mean of 21 min. This figure is in good agreement with observations made at a feeding site which a female regularly visited, where three of its main food plants *(Castilleja, Symbolanthus* and *Pentadenia)* were flowering close together along the edge of a wooded strip. At each visit it remained in the area for 2 to 11 min, during which it went to a favourite perch between feeding bouts. It would then leave, and was absent for 15 to 38 min.

The rather brief observations suggested that, in contrast to the females, male *Lafresnaya* tend to hold feeding territories. On 22 July, a male held a small territory within a wood in which there were many small *Palicourea* trees in the under-storey and 16 open *Pentadenia* flowers near the ground. This bird was seen feeding only at the *Palicourea.* Feeding bouts were frequent, mostly at intervals of 2–16 min. Once it chased a female *Lafresnaya* which intruded, and once a *Diglossa albilatera.* It was probably present for almost the whole of two watches, totalling 2 h 40 min. It was silent when perched in the territory between bouts of feeding, but it uttered the monosyllabic 'seep' when flying round the territory and between probes when feeding. Another male that was watched for an hour in part of a wood that contained only *Palicourea* and a little *Castilleja* seemed to be attempting to infiltrate a territory previously held by a male *Metallura.* It fed silently, mainly on *Palicourea,* and was occasionally chased by another hummingbird, probably the *Metallura.*

In a place where woodland bordered an area of semi-open bushy second growth, with plants mostly not more than 3 m tall, there was intensive activity on three successive mornings among a group of at least 5 *Lafresnaya.* Watches totalling 5 h were insufficient to clarify the nature of the activity, but it was not related to feeding. One male spent much of the time (at least 77 out of 150 min of one watch) on a small group of perches about 10 m up in a tree on the woodland edge overlooking the bushy area. He was regularly visited at this perch by birds in female plumage and occasionally by male-plumaged birds, and these visits usually led at once to long flight chases over the bushy area in which up to three other birds might join. On the perch the male was silent; flight chases were accompanied by bursts of

rapidly repeated calls, 'see-see-see-see . . .', apparently uttered by the bird being chased. This activity suggested an initial stage of some kind of courtship display. Perhaps males group themselves in a 'dispersed lek'; but if so, one would not expect them to be silent on their perches.

Coeligena helianthea

Nearly all our feeding records were of adult males. Females were seen feeding on only two occasions (4 feeding records: *Cavendishia* 2, *Symbolanthus* 1, *Tropaeolum* 1). Males fed predominantly by trap-lining. A few observations suggested that some, at least, spent a good deal of their time at nectar sources that were not within the feeding territories of other hummingbirds, perhaps using them as a base from which to make trap-lining excursions. Aggressive behaviour was seen only once, when a trap-lining male *Coeligena* chased a female *Metallura* that came to a clump of *Passiflora* at the same time as it did. Sixteen intervals between successive visits to the same flowers by what we presumed (from the behaviour) to be the same bird ranged from 16 to 58 min, with an average of 37 min.

Although we had some records of their feeding on small flowers, this fairly large, long-billed hummingbird probably feeds most efficiently from large flowers with straight corolla tubes. At the time of our visit, *Symbolanthus* and *Passiflora* were the only such flowers available. The latter has a corolla tube so long that *Coeligena* cannot probe it legitimately, but instead uses the holes that *Diglossa albilatera* pierces at the base of the calyx. Timed visits of *Coeligena* to *Symbolanthus* flowers lasted from 2 to 9 s, during which up to three probes were made, and visits to *Passiflora* flowers lasted 3–3$\frac{1}{2}$ s.

Ensifera ensifera

We saw *Ensifera* feeding only at the flowers of *Passiflora mixta,* and in fact never saw it except when we were watching at clumps of *Passiflora.* The extraordinarily long bill of *Ensifera,* which exceeds in length the head and body combined, closely matches the corolla tube of *Passiflora.* No other plant that was in flower in the study area approached *Passiflora* in the length of the corolla tube.

Ensifera must be a most pronounced trap-liner. Usually a bird suddenly arrived, fed at the *Passiflora* flowers, and flew straight off. Occasionally it perched briefly near the flowers on arrival, or before flying off. Its feeding visits were few and far between. We watched at *Passiflora* clumps for a total of 23 morning hours (0540–1200 h), in which time we saw 6 visits by *Ensifera.* Four other visits were seen in the morning during watches that were not timed (because attention was not being concentrated solely on the *Passiflora*). Although six of the timed watches were longer than 2 h, and two exceeded 4 h, only once did we see two visits by *Ensifera* during a watch (with an interval of 31 min). Nine of the ten visits were in the periods 0600–0800 and 1000–1100 h.

As has been mentioned, practically all the *Passiflora* flowers that were examined had been pierced at the base by *Diglossa albilatera.* In addition, at least four hummingbird species (and at least one butterfly) took nectar from the holes made by *Diglossa.* Visits by the nectar thieves were regular, and the combined visits were frequent. Thus at the main *Passiflora* clump that was studied a male *Diglossa albilatera* made a thorough round of all the flowers about three times per hour, a female *Metallura* about every half-hour, and a male *Coeligena* about every 40 minutes. Doubtless as a consequence of these frequent visits, *Passiflora* flowers that we sampled at this and other clumps yielded very small quantities of nectar; many gave none that was measurable – in spite of the fact that *Passiflora* flowers produce nectar copiously (Table 2).

In order to determine to what extent *Ensifera*'s food supply was being depleted by the nectar thieves, we protected the bases of a number of *Passiflora* flowers by wrapping them with polythene strips while they were still in bud. The experiment was unfortunately terminated prematurely when we had to leave the Fonté area, but the first results were striking. Visits by *Ensifera* to unprotected flowers were brief, 4 being the maximum number of probes that we recorded. On 19 July, 6 days after several flowers had been protected at the clump

where most observations were made, an *Ensifera* arrived at the clump, went first to three high, unprotected flowers, probed each of them 2 or 3 times, then flew straight down to one of the wrapped flowers (ignoring several flowers that were nearer), probed it ten times, flew straight to another wrapped flower, probed it 9 times, and then flew off. The two protected flowers had opened 1–2 days previously. Even more striking was a visit by *Ensifera* to the same clump on 22 July. On this occasion it went first to an unprotected flower, fed at it for about 2 seconds, then flew to one of the wrapped flowers (not one of those visited on the 19th, which were now over), made 27 probes, perched briefly, and flew off. It seemed that this bird had learnt which flowers were most rewarding, and that one or two flowers could supply as much nectar as it could take on one visit.

Lesbia nuna

The few males that were seen appeared to be holding territories in open areas with scattered trees, not far from woodland edge. They were mostly seen feeding by making aerial sallies for flying insects from tree perches, and only a single visit was seen to a flower (a low-growing *Rubus*). Many more records were obtained for females, which were seen visiting flowers of five species (Table 3).

Particular attention was paid to one female, which defended a small feeding territory centred on a large clump of *Castilleja*. This bird fed mainly within an area measuring c. 25 by 15 m, containing the *Castilleja* clump and, a little separate, a patch of bushy growth including *Castilleja, Palicourea* and *Cavendishia*. At times it moved out onto an adjacent open field and fed on low *Rubus* bushes, and occasionally it moved about 50 m away to feed on *Palicourea* along a wood-edge. Although it ranged over a 25 × 15 m area for most of its feeding, it defended only the large *Castilleja* clump, not attacking the hummingbirds that often came to feed in the bushy patch about 10 m away. Within the defended area it regularly uttered a short, monosyllabic 'zit, zit' while feeding and immediately after returning to the perch. Between bouts of feeding it perched for much of the time on a few favourite perches close to the *Castilleja* clump. During a 2-hour watch from 0730 to 0930 h it spent 39% of the time on these perches, and during a 2-hour watch from 1345 to 1545 h, 48% of the time.

The only other hummingbird seen feeding at the *Castilleja* clump was a female *Lafresnaya*. Although a considerably larger bird, it was regularly chased by *Lesbia nuna* and on several occasions was either prevented from feeding or had its feeding interrupted. Several timings of feeding rates showed that *Lesbia* was consistently less efficient than *Lafresnaya* in feeding at *Castilleja*. On average *Lesbia* visited a flower every 2·7 s (combined figure from records on 3 days, averaging individually 2·8, 2·3 and 3·1), compared with 1·3 s for *Lafresnaya*. This relative inefficiency seemed to result from the fact that *Lesbia* could not hover and probe the *Castilleja* flowers by inserting its bill along the curvature of the corolla, as *Lafresnaya* could. Instead, it probed the flower either by inserting the bill on the under-side, at the point where the corolla tube divides, or by piercing a hole (or using an existing hole) on the upper side of the calyx near the base. Both methods frequently involved clinging to the flower with beating wings.

Chlorostilbon poortmani

This species was seen in only two places, in one of which a male held a feeding territory and was once seen engaged in what appeared to be courtship display with a female. Both were open areas near woodland edge, and the four kinds of plants at which the birds were seen feeding were low-growing herbs or stunted shrubs.

The flower-piercers

Three species of *Diglossa* occurred in the study area, *D. albilatera, D. caerulescens* and *D. carbonaria*. The first two of these occurred mainly in woodland and along woodland edges, while the third was a bird of more open, bushy country. Far the most important of these species, in its effect on the ecology of the hummingbirds, was *D. albilatera,* the smallest of the three and the one whose bill is most highly modified for piercing the base of flowers.

D. albilatera fed very largely on the nectar of *Palicourea angustifolia.* They are small agile birds, and the rate at which they are able to exploit *Palicourea* flowers, about one flower per second, is remarkable. They are regularly attacked by hummingbirds, which clearly recognize them as ecological competitors, and consequently are very furtive, feeding silently and keeping as far as possible to the interior of the plants on which they are feeding.

As already mentioned, the flowers of *Passiflora mixta* were almost invariably pierced by *D. albilatera;* but the proportion of the *D. albilatera* population that fed on *Passiflora* flowers cannot have been very high, as *Passiflora* clumps were sparsely distributed. In contrast to their behaviour at *Palicourea,* they remained for several seconds at *Passiflora* flowers, often piercing them in more than one place, apparently staying until they had extracted all the nectar that they could reach. Although their general behaviour was still furtive, we never saw one attacked while feeding at *Passiflora,* probably because no hummingbirds maintained feeding territories centred on *Passiflora* clumps. The effect of their exploitation of *Passiflora* flowers must have been to reduce greatly the nectar available to *Ensifera,* as discussed above, not only by taking it themselves but also by making available to other hummingbirds a nectar source that would otherwise have been unavailable.

Other flowers seen to be visited by *D. albilatera* were *Cavendishia, Castilleja* and *Symbolanthus* (once each), *Siphocampylus* (twice), a small and apparently rare *Passiflora* lacking a corolla tube, and the introduced foxglove *(Digitalis).* The flowers of *Siphocampylus,* which were just beginning to open when we left the area, are soft and unprotected at the base of the corolla tube, and it seemed likely that their exploitation by *Diglossa* would affect the amount of nectar that they would provide for *Lafresnaya,* their probable main pollinator.

Diglossa caerulescens has a much less specialized bill than *D. albilatera,* and very different habits. Several times we saw single individuals or pairs of *D. caerulescens* accompanying mixed foraging parties of tanagers, flycatchers and other birds. We also saw them eating fruits of *Cavendishia* and *Rubus.* They were recorded visiting flowers of *Palicourea* and *Rubus,* but when they could be observed closely they were seen to enter the flower 'legitimately'. We never definitely saw one piercing a flower.

Diglossa carbonaria, with a bill nearly as specialized as that of *D. albilatera,* was recorded piercing the flowers only of *Palicourea, Cavendishia* and *Manettia.* An individual that held a territory embracing the large *Castilleja* clump at which we spent watches totalling 11 h, showed no interest in the *Castilleja* flowers though it sometimes perched close to them. This species is considerably larger than *D. albilatera* and is not so subordinate to hummingbirds, though its behaviour in approaching and working through vegetation in search of flowers is similarly furtive. Once one was seen to drive an *Eriocnemis vestitus* from a *Cavendishia* flower, and once one was attacked by *E. vestitus* while feeding at *Cavendishia* but was not dislodged.

Observations at Carare

Vegetation, and available nectar sources

Most observations at Carare were made along $1\frac{1}{2}$km of forest path at a height of 2300 to 2450 m. The path ran through an extensive area of forest some $2\frac{1}{2}$ km wide, extending from the ravine of the Rio Uvasa (2000 m) to the top of a steep cliff (Las Alturas, 2800 m) and probably beyond. There had been recent and old selective felling in the forest but apparently no clear felling. In addition observations were made in adjacent open country, some of which was naturally unforested being poorly drained and boggy but most had been cleared and probably regularly burnt. These open areas were at 2200 to 2300 m, with a small area of about 2 ha at 2450 m.

In the forest 20 species of plants and in the open areas 4 species were seen to be visited for nectar by hummingbirds in $10\frac{1}{2}$ days of observation. Of these 24 species, 9 were climbers including the scrambling tree heaths, 7 were woody shrubs, 4 were herbaceous ground-living plants, 3 were trees, and one was an epiphyte (Table 5). Considered by families, the

Table 4 Characteristics of hummingbird flowers, Carare

Family	Species	length of tube (mm)	Corolla colour	orientation[1]	concentration[2] %	Nectar production[3] µl
Guttiferae	*Clusia* sp.[4]	nil	cream	U	15–17, 16·0	20 (12 h, night)
Ericaceae	*Cavendishia cordifolia*	15	pink & white	H–P	9–22, 14·9[5]	22 (24 h)
	Cavendishia guatapeenis	10	red	P	19	17·5 (24 h)
	Cavendishia pubescens	31	pink	P	12–21, 16·1	26 (24 h)
	Disterigma sp.[4]	8	white	H	22–41, 27·8	2·5 (24 h)
	Psammisia falcata	29	orange	P	11–18, 14·3	16·2 (8 h, daytime)
	Thibaudia rigidiflora	21	orange-pink	P	13–24, 17·6	9·2 (14 h, night)
Leguminosae	*Phaseolus coccineus*[4]	—	red or white	—	27–45, 35·7	5·0 (5 h, morning)
Melastomataceae	*Huilaea macrocarpa*	(open bell)	red	P	12–16, 13·4	15·5 (2 h)
Gentianaceae	*Macrocarpaea* sp.	(open bell)	cream	P	—	—
Acanthaceae	*Aphelandra* sp.[4]	30	orange	U	24–28, 25·4	5·5 (24 h)
Campanulaceae	*Burmeistera globosa*	30	green	H	10	20 (24 h)
Rubiaceae	*Manettia* aff. *sabiceoides*[4]	11	white	H	25–26, 25·5	3·9 (24 h)
	Palicourea demissa	31	purple-pink	P	14–18, 16·0	46 (24 h)
	Palicourea cf. *vagans*[4]	9	white (calyx yellow)	H	23	3·2 (24 h)
	Palicourea sp. 43[6]	15	yellow (calyx red)	H–P	20–22, 21·0	1·8 (2 h)
	Posoqueria sp.	67	white	H	15–21, 17·0	—
Bromeliaceae	*Guzmania cryptanta*	30	white (bract red & yellow)	U	20–22, 21·0	81 (24 h)
	Pitcairnia sp.	—	white	H	—	—
	Tillandsia aff. *turneri*	36	yellow (bract red)	H–U	18–20, 19·3	98 (24 h)
Amaryllidaceae	*Bomarea* cf. *carderi*	—	pink & green	P	11–17, 13·7	46 (24 h)
Orchidaceae	*Elleanthus smithii*	11	cream & pink	H	8–22, 14·8	7·1 (24 h)

Notes: [1] H = horizontal; P = pendent; U = upright.
[2] range and mean. Single figures indicate single measurements.
[3] amount produced over period indicated in brackets.
[4] also visited by insects.
[5] measurements from Fonté.
[6] collection number; specimen in herbarium of Instituto de Ciencias Naturales, Universidad Nacional, Bogotá.

Ericaceae with 6 species (27% of total nectar records), the Rubiaceae with 5 species (16% of total nectar records) and the Bromeliaceae with 3 species (15% of total nectar records) were making the biggest contribution to hummingbird nectar resources during our visit. Only single members of other families were utilized for nectar.

Herbaceous plants

In the unforested areas two herbaceous ground plants were important and rich sources of nectar: *Guzmania cryptanta,* a bromeliad associated with boggy areas, and an orchid, *Elleanthus smithii,* which grew on dry rocky ground. Both had inflorescent spikes with flowers presented in an upright or horizontal position (Table 4), but the *Guzmania,* with a much longer corolla, produced over ten times more nectar per 24 hours.

At the first visit (31 July to 3 August) the *Guzmania* growing at 2300 m was half over but it was in full flower (average of c. 7 flowers per plant) at 2450 m. Here it grew quite densely, a sample area of c 30 × 20 m containing 139 plants with flowering spikes. By 15 August only 17 of these 139 spikes were still flowering, with a total of only 42 flowers. *Elleanthus* was only just beginning to flower at the first visit but was in full flower at 2200 m between 14 and 21 August. Here it grew extremely densely: an area measuring 1 × 5 m contained 24 flowering spikes and many other equally dense stands were nearby.

The two other open country plants were the ground bromeliad *Pitcairnia,* growing rather sparsely at the edges of bog and forest, and the heath *Cavendishia cordifolia* which grew as a very low shrub (30–60 cm) and was fruiting rather than flowering during our visit. All the remaining 20 species were associated with the forest except the runner bean *Phaseolus coccineus* which was a weed in recent forest clearing.

Trees

The flowering strategies of the three trees were completely different; probably only *Huilaea macrocarpa* has coevolved with hummingbirds. *Posoqueria* sp. is a small under-storey tree 6–10 m tall. Its large, sweet-scented white flowers with long, 67 mm corollas are presumably adapted for pollination by night-flying moths with long prosbosces. When a small tree was cut down at 1340 h in order to examine the flowers, four anthers pressed together blocked the entrance to the tubular corollas but these anthers sprang open when pushed by a pipette. *Posoqueria* flowers were only visited by hummingbirds early in the morning, the short-billed species obtaining their nectar through pierce holes at the base of the corolla.

Clusia grew in patches of secondary forest, reaching a height of 8–12 m. Trees in full flower bear masses of abundantly staminate, cream-coloured flowers, whose corollas are open shallow cups. Individual flowers open early in the morning and are over by evening. On opening, flowers were found to contain an average of c. 20 µl of nectar. Many insects and different species of hummingbirds visited the *Clusia* flowers, particularly in the early morning.

Huilaea was a common under-storey tree growing to a height of 14 m. Seven trees examined showed all stages of flowering and fruiting on each tree, and it looked as if the species might have a continuous flowering regime throughout the year or at least for the greater part of the year. The flowers are large, open, pendent red bells; the pedicel is long and the calyx is a hard woody hemisphere. Flowers *in situ* were too high to be reached; but three obtained by cutting down the limb of a small tree contained 9·5–22 µl (average 16·5 µl) of nectar. One, bagged at 11·00 h, contained 15·5 µl of 13% nectar 2 h later. Individuals of *Boissoneaua flavescens* were territorial at all the *Huilaea* trees that were watched. No insects or flower-piercers were seen to visit the flowers.

The following characteristics of *Huilaea* indicate that it is adapted for hummingbird pollination: the large pendent red flowers (p. 134) with copious nectar of low sugar concentration (p. 137), the woody calyx (protecting the nectaries from nectar-thieves – p. 134), and the long flowering season (which ensures a long-term nectar supply for a reliable, long-lived pollinator). It is noteworthy that *Huilaea* is a monotypic genus known only from the

Colombian Andes, and belongs to a family (Melastomataceae) whose species are typically insect-pollinated.

The Ericaceae

The Ericaceae showed examples of different flowering strategies, both for attracting pollinators and for avoiding flower-piercers. Within the forest the abundant *Disterigma* sp., a shrub up to 2 m in height, was flowering plentifully at both visits. Its many small white flowers are evenly scattered all over the densely growing shrub; the flowers are presented horizontally and produce small amounts of concentrated nectar (Table 4). It is much visited by bees, which are presumably its pollinators. Although short-billed hummingbirds, particularly the very small *Adelomyia,* fed at it, this heath appears not to have evolved away from the hymenopterophilous syndrome. *D. albilatera* was once seen at it, but only 2 out of 25 flowers examined had pierce holes. Presumably such dispersed, small amounts of nectar, also available to insects, are not an attractive food source for flower-piercers.

No insects were seen to visit the two scrambling tree heaths *Psammisia falcata* and *Thibaudia rigidiflora*. Both have pendent bright pink or orange flowers with long corollas which bloom in dense ranks along horizontal woody stems or twigs. The corollas are unprotected and 71% of 58 flowers of *P. falcata* and all of 10 *T. rigidiflora* flowers examined had been pierced at the base. *D. albilatera* was frequently observed piercing the corollas of both plants. These two heaths appeared to have different flowering seasons, a characteristic of related ornithophilous plants (Stiles 1975, 1978). Thus *P. falcata* was in full flower at the lowest forest levels (2350 m) during both visits but not flowering at higher levels, while *T. rigidiflora* was not flowering inside the forest at either visit but at the second visit a few flowers were out at the forest edge at 2350 m and an isolated bush in cleared land at c. 2250 was in full flower. *Psammisia* was an important source of nectar for *C. prunellei* and *Doryfera,* and the former was also seen to feed at *Thibaudia*. A characteristic of these heaths is the dense packing of stamens, particularly in *Psammisia,* so that in the latter it requires some pressure to push a micropipette more than 19 mm down the corolla tube. Possibly this serves to exclude all but a few hummingbird species, and so increases the likelihood of out-cross pollination.

The three *Cavendishia* species present their flowers clustered together in groups of from 5 to 13 flowers, with the base of the corollas enclosed by several layers of leaf-like bracts. In *C. pubescens* the bracts are thick and densely covered with hairs, the clusters are pendent and the corollas long (31 mm). This species was an important nectar source for *Doryfera* and *Coeligena torquata,* both long-billed trap-lining hummingbirds. Only one out of 13 flowers examined had a pierce hole in the corolla and no flower-piercers were seen feeding at them.

C. guatapeensis had nearly finished flowering at the time of our visit, so observations were few. Its flower clusters are pendent and the corollas short (10 mm); they were not examined for pierce holes. Both long- and short-billed hummingbirds were seen to feed at them, but no insects were noted.

C. cordifolia was found only as a low-growing shrub on cleared rough land and on the forest fringes; it was mainly fruiting at the time of our visit and had few flowers. *C. cordifolia* flowers have shorter bracts than *C. pubescens* and the corolla tubes are readily pierced by *Diglossa albilatera;* only a small number were examined but all were pierced. The flowers are orientated between horizontal and pendent, and the corolla tube averages 15 mm in length. At Carare two short-billed hummingbirds were seen to feed at it; at Fonté all the hummingbirds except *Ensifera* fed at it.

While all three *Cavendishia* species are visited and probably pollinated by hummingbirds, *C. pubescens* shows the most advanced adaptations for hummingbird pollination, i.e. the highest nectar production per flower, restriction of nectar to long-billed hummingbirds (indicating coevolution with specialist pollinators – see p. 134), and adequate protection of the nectar from flower-piercers.

The Rubiaceae

Hummingbirds visited five species of Rubiaceae, one of which *(Posoqueria)* has already been described. Two species, *Manettia* aff. *sabiceoides* and *Palicourea* cf. *vagans,* were visited by bees as well as by hummingbirds. Both have features typical of bee-pollinated flowers: white corollas 9–10 mm long presented horizontally, each flower containing a small volume of nectar of relatively high concentration (23–25.5%). The *Manettia,* which also grew at subtropical altitudes at Togui, has no ornithophilous features. The small white flowers with green calyces are scattered evenly all over the plant. Only two very small hummingbirds were seen feeding at it, *Ocreatus underwoodi* at Carare and *Chlorostilbon gibsoni* at Togui. Both were only seen to feed early in the morning and there was good evidence that *C. gibsoni* stopped feeding when bees became active and began to feed at it (see p. 133). *Palicourea* cf. *vagans* shows some ornithophilous characters: the flowers are visually more conspicuous as the calyx is yellow, and they grow in a loose panicle. Spatial concentration of the flowers probably makes them less energetically costly for a hummingbird to exploit. This *Palicourea* was an extremely common small shrub and seven species of hummingbird were seen to feed at it at various times of day; 82% of nectar records were from species with beak lengths of 18 mm or less.

The two remaining species of Rubiaceae, both *Palicourea,* show many more ornithophilous characters. *Palicourea* sp. 43 was a large shrub or small tree growing to a height of 5 m. The flowers are borne in loose panicles, orientated between horizontal and pendent. The tubular corolla is yellow, averaging 15.4 mm in length, and the calyx is red. The nectar could only be sampled by cutting down a small limb. If the nectar secretion which accumulated 2 hours after the limb was cut is typical (Table 4), the quantity per flower is high. Two shrubs formed the feeding territory of a male *Heliangelus.* During watches totalling 3 h on two mornings it fed almost exclusively at these shrubs and drove off a *Diglossa albilatera* which attempted to feed at them.

Palicourea demissa shows the most advanced ornithophilous characteristics. The purple flowers, borne in groups, have long pendent tubular corollas and abundant nectar of low concentration. The corolla is thick and fleshy, probably for the protection of the nectar from flower-piercers, which were not seen to visit the flowers in 4 h of watching. *P. demissa* is a woody scrambler and was found flowering as low as 1 m in disturbed forest and at 10 m in undisturbed forest. Many of these characteristics suggest convergence with tree-heaths such as *Psammisia* and *Thibaudia,* and in fact they share the same *Coeligena* pollinators (Table 5). There was good evidence that short-billed hummingbird species such as *Adelomyia,* *Boissoneaua* and *Heliangelus* did not visit *P. demissa,* nor was it visited by insects.

Other plants

Of the remaining plants, three climbers and two shrubs, only one appeared to be adapted for hummingbird pollination, the climber *Bomarea* cf. *carderi.* This was abundant and in flower at 2350 m, and was also flowering but less abundant at higher levels. The inflorescence is a cluster of pendent flowers with long pedicels. Each flower is tripetalous, with nectaries at the base of each petal. The nectar is abundant and of low concentration. The basal portion of the petal is rolled up and joined to form a long thin tube, which is so narrow that it is impossible to insert a fine pipette (c. 0.6 mm external diameter) into it. The nectar is thus available only to hummingbirds with long thin bills that can hover and exert some upwards thrust, an ability similar to that needed for feeding at the heath *Psammisia.* Only *Coeligena torquata* was seen to feed at it. *C. prunellei,* a thicker-billed bird, is probably unable to reach the nectar as it was frequently seen to fly past and ignore it.

Aphelandra sp., a climber with conspicuous orange flowers, was visited by large bees as well as by hummingbirds, and may be primarily bee-pollinated. It has the following characteristics associated with bee rather than hummingbird pollination: flowers pointing more or less upwards; tubular corolla enlarging at the mouth, with a lower landing lip; and small quantities (5.5 µl) of high concentration (25%) nectar. In spite of its long corolla its nectar is available to such short-billed hummingbirds as *Adelomyia, Heliangelus* and

Aglaiocercus, probably because the wide end of the corolla enables these species to insert part of their heads into the mouth of the flower.

Feeding ecology of the hummingbirds

Of the 12 species of hummingbirds recorded at Carare, all but two were resident and seen every day that watches were kept on appropriate flowers. The two exceptions were *Acestrura mulsant*, which was seen on four occasions between 1 and 3 August but not at all between 14 and 21 August, and *Aglaiocercus kingi*, which was seen on only three of the possible $10\frac{1}{2}$ days of observation.

Nine of the 10 regular species can be subdivided into four groups: two small forest species with short bills and wings, *Adelomyia melanogenys* and *Ocreatus underwoodi*, most of whose nectar flowers had short corollas and were also visited by insects, mainly Hymenoptera; two behaviourally similar forest species with long wings and short bills, *Boissoneaua flavescens* and *Heliangelus amethysticollis*, which combined territoriality over concentrated nectar resources with a high percentage of insect-feeding by hawking; three long-billed woodland species, *Coeligena prunellei*, *C. torquata* and *Doryfera ludoviciae*, all of which were trap-liners, largely feeding on specialized hummingbird flowers; and two non-woodland species, *Colibri coruscans* and *Chlorostilbon poortmani*, only seen feeding in open areas. The tenth species, *Colibri thalassinus*, was seldom seen feeding, although a total of seven individuals with tree-top song posts along forest-edges were regularly present and sang throughout the day. The few feeding records were from forest openings or edges.

The feeding records for hummingbirds at Carare are summarized in Table 5.

Adelomyia melanogenys
Ocreatus underwoodi

Both species were confined to the forest. *Adelomyia* was probably the most abundant forest hummingbird; *Ocreatus* appeared to be considerably less abundant, as indicated by the number of feeding records (Table 5), but the difference may be due in part to the height at which if fed, 4–7 m (mean 3.2) compared with 0.6–7 m (mean 1.4) in *Adelomyia*, as small hummingbirds feeding high up, especially in the crowns of trees, are difficult to see. *Ocreatus* was also seen hawking for insects at a height of 10 m.

Eighty-three per cent of the nectar records for *Adelomyia* were from flowers at which insects, mostly Hymenoptera, also fed (the probably night-flowering *Posoqueria*, which it exploited through pierce-holes, is excluded). The seven flowers with tubular corollas that it visited had effective corolla lengths of 8–30 mm, (mean 14.2), and none of them were pendent. *Adelomyia* was not basically territorial but appeared to be trap-lining over considerable distances, mainly to flowers with small amounts of nectar (e.g. *Disterigma*) which would be uneconomic for the larger trap-lining hummingbirds to visit, or to plants where the amount of nectar per flower was higher but only a few flowers were blooming per plant (e.g. *Palicourea* sp. 43). Timed intervals between return visits to the same flower were 13 min for *Aphelandra* and 26 min for *Palicourea* cf. *vagans*. The times spent at each flower were generally extremely short. Territorial behaviour (calling while feeding) was noted only from a bird feeding in a small forest clearing at *Phaseolus* flowers that were also being visited by *Chlorostilbon poortmani*, and from a bird feeding in the early morning at the pierce holes of *Posoqueria* flowers in company with conspecifics and *Ocreatus*. An *Adelomyia* was repeatedly driven away from profusely flowering *Palicourea* sp. 43 by a territorial *Heliangelus*.

Three out of the four flower species visited by *Ocreatus* (omitting *Posoqueria*, which it exploited through pierce holes) were also visited by insects. *Ocreatus* visited flowers with short corolla tubes that were not pendent (effective corolla lengths 9–15 mm, mean 11.7) and open cup flowers such as *Clusia* sp. It was only seen visiting *Clusia*, where there was much territorial activity between many large hummingbirds, after the early morning peak of feeding activity. The only encounters seen were with conspecifics at *Clusia*, and when it was chased by *Adelomyia* at *Posoqueria*.

Boissoneaua flavescens
Heliangelus amethysticollis

These two species have short bills in relation to their wing-lengths, especially *Boissoneaua* whose bill is only 23% of its wing-length (Table 1). As discussed later (p. 136), this is characteristic of territorial species, and it may also be associated with efficiency in hawking for insects, a method of feeding that was important for both species.

Boissoneaua and *Heliangelus* were to a large extent separated by the height at which they fed. The average height of the 56 nectar-feeding records for *Boissoneaua* was 8·1 m (range 3–12 m), and that of the 34 records for *Heliangelus* 2·8 m (range 0·6–6 m). These height differences were mainly due to the fact that the feeding territories of *Boissoneaua* were based on *Huilaea* trees, whose flowers were mainly at 6–12 m, whereas one of the two feeding territories of *Heliangelus* was based on a patch of ground bromeliads *(Guzmania cryptanta)* and the other on shrubs of *Palicourea* sp. 43, whose flowers were at 1·5–5 m. The heights at which they hawked for insects differed in the same way, *Boissoneaua* usually making long sallies of up to several metres from high perches (mean perch height for 96 sallies 8·6 m, range 2–14 m) while *Heliangelus* made short sallies of 1 m or less from low perches (mean perch height for 20 sallies 2·8 m, range 2·5–3 m).

Boissoneaua and *Heliangelus* have in common two behavioural characteristics associated with territorial defence. One is to hold both wings open and vertical above the back for about half a second after landing. Thus a *Boissoneaua,* after an encounter with a conspecific, fed at five *Huilaea* flowers on one tree, perching briefly with wing display after each feed. When no encounter had taken place for the previous 40 min, a *Boissoneaua* perched four times with wing display during a feeding bout lasting 1 min 9 s, during which 21 *Huilaea* flowers were visited. In a typical instance a male *Heliangelus,* 8 min after chasing an *Adelomyia* from its feeding territory, perched briefly with wing display eight times during a feeding bout at a single bush of *Palicourea* sp. 43 lasting 1 min 39 s. Secondly, both species periodically circle part of their feeding territory in level flight uttering a trilling call. These circular flights were made at heights of 4–6 m by *Boissoneaua* and about 3 m by *Heliangelus.*

Boissoneaua fed mainly at mid to canopy levels in the forest, including the canopy-flowering *Clusias* that grew in places along the forest edge. As well as conspecifics, it was seen to drive *Heliangelus, Colibri coruscans* and *Chlorostilbon poortmani* from its feeding territories. It failed to drive off a *Coeligena prunellei* (from *Huilaea*) but made vigorous attempts to do so.

The four flowers with tubular corollas which it visited had effective corolla lengths of 8–15 mm (mean 10·7). Three out of the seven flower species which it visited were also visited by insects, but these three accounted for only 29% of nectar records. During our visit the under-storey tree *Huilaea macrocarpa* was undoubtedly its most important source of nectar (66% of all nectar records). Eight different *Huilaea* trees found flowering in four different areas were all centres of *Boissoneaua* feeding territories and except for one record for *Coeligena prunellei* no other hummingbirds were seen feeding at them in a total of 5 h of watching.

Some individual *Boissoneaua,* apparently with compact territories, continually uttered a repeated *sip sip,* at an average rate of 30 *sips* per minute, when in their territories except while they were on the wing nectar-feeding or hawking for insects. One such individual, watched for 1 h on a sunny but rather windy afternoon, called for 91% of the time. For the remainder of the time, except for 1 min 34 s when it was not in view, it made 9 hawking sallies and 10 visits for nectar to a total of 13 *Huilaea,* 9 *Disterigma* and 8 *Palicourea* cf. *vagans* flowers. Another 1 h afternoon watch on the same individual, when the weather was overcast and still in the first half of the watch and slightly breezy in the second half, gave the following results: first ½ h, 41 insect-hawking sallies and 4 nectar visits to a total of 5 *Huilaea* flowers, average interval between visits 8·7 min; second ½ h, 33 insect-hawking sallies and 5 nectar visits to a total of 10 *Huilaea* flowers, average interval between nectar visits 5·8 min. It was evident that the still overcast weather was the more suitable for insect hawking and an indication that even a slight breeze may decrease the profitability of such an activity. The

Table 5 Hummingbird feeding records, Carare

	D.l.	C.th.	C.c.	C.po.	A.me.	C.pr.	C.to.	B.f.	H.a.	O.u.	A.k.	A.mu.
Herbaceous plants, ground												
Guzmania cryptantha		6	19	11					8			1
Pitcairnia sp.			2	2								
Elleanthus smithii			19		3							
Herbaceous plants, epiphytic												
Tillandsia aff. turneri						9						
Vines/climbers												
Cavendishia pubescens	5											
Psammisia falcata	14					28	8					
Thibaudia rigidiflora						1						
Phaseolus coccineus				4	15							
Aphelandra sp.					2	5						
Manettia aff. sabiceoides									1		1'	
Palicourea demissa						11	1			2	2	
Bomarea cf. carderi							3					

Table 5 Hummingbird feeding records, Carare (cont.)

	D.l.	C.th.	C.c.	C.po.	A.me.	C.pr.	C.to.	B.f.	H.a.	O.u.	A.k.	A.mu.
Woody shrubs												
Cavendishia cordifolia				1								
Cavendishia guatapeensis					1		1	1				
Disterigma sp.					2			4	4			
Macrocarpaea sp.					11	5	1					
Burmeistera globosa						1						1
Palicourea cf. *vagans*					6	2	2	5	3	3		
Palicourea sp. 43	2				1	1	1	2	13	1		
Trees												
Clusia sp.		19	12		1			7	5	2	1	
Huilaea macrocarpa						1		37				
Posoqueria sp.					5[1]	1				1[1]		
Other plants					2							
Insect-hawking		2	1			3	1	96	20	1		1
Insect-gleaning				1		1	1	1				
Totals (481)	21	27	53	19	49	69	19	153	54	10	4	3

Hummingbirds abbreviated as follows: *A.k.*, *Aglaiocercus kingi*; *A.me.*, *Adelomyia melanogenys*; *A.mu.*, *Acestrura mulsant*; *B.f.*, *Boissoneaua flavescens*; *C.c.*, *Colibri coruscans*; *C.po.*, *Chlorostilbon poortmani*; *C.pr.*, *Coeligena prunellei*; *C.th.*, *Colibri thalassinus*; *C.to.*, *Coeligena torquata*; *D.l.*, *Doryfera ludoviciae*; *H.a.*, *Heliangelus amethysticollis*; *O.u.*, *Ocreatus underwoodi*.

Note: [1] nectar taken 'illegitimately', through pierce holes.

lack of records on the second afternoon from *Disterigma* and *Palicourea* cf. *vagans,* with their small nectar rewards compared to *Huilaea* (Table 4), suggests that they may be visited only when there is insufficient food available from other sources.

Heliangelus is an aggressive territorial species of forest and forest edge. In two morning watches totalling 2 h 50 min a male with a territory centred on two *Palicourea* sp. 43, drove off *Adelomyia* seven times, *Coeligena torquata* twice, and a *Doryfera* and *Diglossa albilatera* once each, all of which were attempting to feed at the *Palicourea.* It was unable to keep *Boissoneaua* from the *Palicourea* although it persistently attempted to.

During an 80-min morning watch this male spent 9% of the time feeding, 4% chasing intruders, and 61% perched in the territory; the remainder of the time it was out of view. During another 90-min morning watch it spent 11% of the time feeding, all but 30 s at *Palicourea* sp. 43 (corolla length 15 mm). During these watches *Heliangelus* never visited two profusely flowering plants of *Palicourea demissa* (corolla 31 mm) which were only 2–3 m from its main perch in *Palicourea* sp. 43. During a 40-min watch where *Cavendishia* cf. *pubescens, Palicourea* cf. *vagans* and *Disterigma* sp. were growing close together and could be simultaneously watched, *Heliangelus* came twice to visit the *Palicourea* and *Disterigma* (corollas 9 and 8 mm), by-passing the *Cavendishia* (corolla 31 mm). It is probably not just its short bill which prevents *Heliangelus* from feeding at such flowers as *P. demissa* and *C.* cf. *pubescens,* as one held a feeding territory over a group of the ground bromeliad *Guzmania* whose flowers have long corollas (30 mm) but grow at an angle between upright and horizontal. Probably the pendent growth of the former two flowers is the main factor preventing *Heliangelus* from feeding at them.

Coeligena prunellei

Of the three long-billed trap-liners, *C. prunellei* was the most abundant and was seen to visit the greatest number of different flower species. It is the largest in wing length and weight (Table 1), but compared with the other two species in this group its bill averages 3 mm shorter, and is appreciably stouter.

Seventy per cent of the nectar records for this species were from vines or climbers, including the climbing tree heaths (i.e. *Psammisia falcata, Thibaudia rigidiflora, Palicourea demissa* and *Aphelandra* sp.), all of which were flowering in undisturbed forest near canopy level and at much lower levels in disturbed forest and clearings. *C. prunellei* visited these flowers at both levels. The bromeliad *Tillandsia* aff. *turneri,* to which only *prunellei* was seen to go, was epiphytic on trees at heights of 5–12 m (mid to lower canopy levels).

C. prunellei fed mainly by trap-lining. Mean intervals between successive visits to the same flowers were as follows: at profusely flowering *Psammisia* 23 min; at *Palicourea demissa* 40 min; and at well-spaced single plants of *Tillandsia* 44 min. In places where selective felling had greatly increased the growth and flowering of such heaths as *Psammisia falcata* and so provided a concentrated nectar source, it occasionally perched nearby and showed territorial activity, chasing off *Doryfera* (5 chases in $3\frac{1}{2}$ hours watching) which was the only other species seen feeding at this flower. Out of a total of 47 feeding records it was silent while feeding except on four occasions when it uttered a monosyllabic 'ick' between probes. Typically, calling while feeding is characteristic of territoriality; its infrequency in *prunellei* suggests that this is not a common strategy. Although competition with its congener *C. torquata* might have been expected, only one encounter was seen when *prunellei* chased *torquata* from the vicinity of *Palicourea demissa.* Results of encounters between the two *Coeligenas* and other species of hummingbird suggest that *torquata* is always subordinate to the slightly larger *prunellei.* The lack of encounters observed between them was due to the fact that no nectar feeding was recorded for *prunellei* above c. 2400 m, whereas all but two of the records for *torquata* were above this level. The heath *Psammisia* was abundant and in full flower at 2350 m; at higher levels it was present but the flowers were not open. As *Psammisia* appeared to be the most important nectar source for *prunellei,*

this was probably the underlying reason for the partial altitudinal separation of the two *Coeligenas*.

Except for three records of *prunellei* visiting the two *Palicoureas* with short corolla tubes (9 and 15 mm), the seven plants with tubular corollas which it visited have long corolla lengths, (21–67 mm, mean 34·9). Seventy-two per cent of all nectar records were from plants whose flowers are pendent so that the hummingbird needs to hover upwards into them. In addition the flowers of two of the heaths are so full of stamens as to require considerable upward pressure to penetrate them. The following evidence suggests that other hummingbirds are unable to utilize these heaths. In 11 hours of watching at six different plants of *Psammisia* only *prunellei* and *Doryfera* came for nectar except for one visit to pierce holes by *Aglaiocercus kingi*. During 3½ hours of watching at various times of day at a profusely flowering bush of *Thibaudia* left by clearance c. 200 m from the nearest woodland, only *Diglossa* fed at its nectar although the two open country hummingbirds *C. poortmani* and *C. coruscans* were both seen perching on it at different times. On the other hand *prunellei* seemed to be unable to exploit the flowers of *Bomarea* cf. *carderi*, which were an important nectar source for the slender-billed *C. torquata* (see below). In the course of 3 h of watching at a place where *B.* cf. *carderi* and *Palicourea demissa* could be watched simultaneously, *prunellei* went six times to the *Palicourea* but did not visit the *Bomarea*.

Coeligena torquata

C. torquata, the longest-billed of the Carare hummingbirds, was a silent, trap-lining nectar feeder confined to the forest, where it was recorded feeding at heights of 1–12 m (mean 5·2 m). It was chased by *C. prunellei* and *Heliangelus*, and was seen to be aggressive only to conspecifics. Records were few and it appeared not to be so abundant as *C. prunellei*, particularly at lower elevations. Like the latter it largely (76% of all records) went to pendent flowers with long corolla tubes at which insects were not recorded. On occasions when *Palicourea* cf. *vagans*, with a short corolla, and *Cavendishia* cf. *pubescens*, with a long corolla, could be watched simultaneously, in a total of 2½ h it entirely ignored the *Palicourea* and went only to the *Cavendishia*. This was the only species seen feeding at *Bomarea* cf. *carderi*, a flower that was avoided by *C. prunellei* (see above).

Doryfera ludoviciae

This species was a pronounced trap-liner, showing no evidence of territorial behaviour. Adults were mainly seen foraging at the heaths with long pendent corollas; their extremely fine pointed bills are probably well fitted for probing this kind of flower, which they exploited at the rate of 0·8 s (*Cavendishia* cf. *pubescens*) and 0·9 s *(Psammisia)* per flower (cf. 1·4 s per flower for *C. prunellei* at *Psammisia*). They were frequently seen to be dominated by *C. prunellei* and occasionally by *Heliangelus*.

Feeding records for two juveniles which were still being fed by a parent are omitted from Table 5. For 10 days these two juveniles were sedentary in a small area of thick undergrowth measuring about 10 by 4 m, where they supplemented parental feeds by feeding at *Disterigma* (16 records) and *Cavendishia guatapeensis* (3 records). They were also seen hawking for insects three times. They appeared to drive *Adelomyia* from the *Disterigma* in this area, but possibly the apparent attacks were mistaken food-begging.

Colibri coruscans

C. coruscans was only seen in open areas where it was highly territorial and vocal. At our first visit to Carare (31 July to 3 August) all the *coruscans* feeding territories were centred on the ground bromeliad *Guzmania cryptanta*, which was then probably at its peak of flowering. By 15 August only 12% of the *Guzmania* were still flowering and no *coruscans* held territories over them, but some were singing and holding feeding territories over the orchid *Elleanthus smithii*, mostly at 2200 m where it was flowering profusely in dense stands. Among the extensive boggy areas at 2450 m where the *Guzmania* grew, were wooded islands with *Clusia* trees which were flowering at both visits. At the first visit *coruscans* was

frequently foraging at these *Clusias,* which appeared to form part of their feeding territories. At the second visit when the *Guzmania* was largely over, visits by *coruscans* to *Clusia* were intermittent and they were not singing in the area. Territorial *coruscans* sing almost continually and frequently call between probes while feeding. Most encounters were between conspecifics, but they were also seen chasing *C. thalassinus* from *Clusia* and were themselves driven from this tree by *Boissoneaua.*

They frequently perch while feeding at *Guzmania* and *Elleanthus* and occasionally do so at *Clusia.* It is probably of significance that the four plant species at which *coruscans* foraged present their flowers either in an upright or horizontal position (Table 4); no feeding was recorded at pendent flowers.

The smaller *Colibri thalassinus* was seen foraging at two plants, *Guzmania* and *Clusia.* The *Guzmanias* at which it was seen to feed were either in small forest openings or close to the forest edge; it was never seen feeding well out in cleared areas, as was *coruscans.* *C. thalassinus* was recorded feeding at *Clusia* in the second period of observations, when most of the *coruscans* had descended to lower elevations to hold territories at the *Elleanthus.* It appeared to be more sedentary than *coruscans,* and seven singing males occupied the same song posts throughout both periods of observation.

Chlorostilbon poortmani

C. poortmani was common in open areas, where it fed at *Guzmania* and *Elleanthus* flowers. When *Guzmania* was largely over and abandoned by *Colibri coruscans, poortmani* continued to feed at the sparse flowers. It also fed in recent forest clearings on the bean *Phaseolus.* It foraged at heights of 0·6–4 m (mean 1·1 m) and often called in flight between nectar sources, but not while feeding. Except for a record at *Cavendishia cordifolia* it fed at flowers whose corollas were orientated between horizontal and upright. *C. poortmani* was not seen engaging in territorial encounters, but behaved as a trap-liner of scattered resources in unforested country.

Observation at Togui

Vegetation, and available nectar sources

The impoverished flora of the hacienda near Togui included 11 plant species which were providing nectar for hummingbirds at the time of our visit (Table 6, which also includes two other plant species found in cultivated country beyond the bounds of the hacienda). Far the most conspicuous was the introduced tree *Eugenia jambos,* which grew mainly along river banks and in hedges between pastures. Introduced plants *(Eugenia, Musa* (banana), *Ipomoea* sp. and *Canna indica)* accounted for 77% of all records of nectar feeding.

Eugenia jambos, with its copious nectar of low concentration, was the main nectar source for all the hummingbird species except for *Phaethornis guy* and *Chlorostilbon gibsoni,* which were not recorded at it. Many species of butterflies and other insects also fed at it. Butterflies were observed feeding between 0822 and 1521 h, bees between 0720 and 1615 h. Nectar rewards for hummingbirds must have been highest in the early morning and late evening; they were recorded feeding at *Eugenia* between 0605 and 1806 h, with peaks in the morning and evening.

Guzmania sp., an epiphytic bromeliad, grew high in the trees with its 1·5 m inflorescence stem often reaching up into the crown. It was abundant, but only one plant was found with flowers, which were visited by *Amazilia cyanifrons,* apparently the most pronounced aboreal feeder of the hummingbirds present. Small bees go to the rim of the tubular corolla of this *Guzmania* but do not enter it. Individual flowers last less than 24 h and produce nectar with an average concentration of 17·8%, a typical figure for hummingbird-pollinated flowers. The four other plants with mean nectar concentrations between 14 and 19% (Table 6) also have visual or morphological characters typical of hummingbird flowers, i.e. pink, red or orange colours in or near the inflorescence (all species), and tubular corollas which are pendent or

Table 6 Characteristics of hummingbird flowers, Togui

		Length of tube (mm)	Corolla colour	orientation[1]	Nectar concentration[2] %	Nectar production[3] μl
Ericaceae	*Cavendishia pubescens*[4]	19	pink	H–P	15–20, 17.7	—
	Psammisia penduliflora	15	red	P	10–18, 15.0	2·0 (18 h)
Leguminosae	*Calliandra purdiei*	nil	pink & white	U	—	—
Myrtaceae	*Eugenia jambos*[5]	nil	cream	U	6–17, 9.7	47 (24 h)
Apocynaceae	*Mandevilla* aff. *mollissima*[5]	25	green & white	H	—	—
Convolvulaceae	*Ipomoea* sp.[5]	—	pale pink	H	16–46, 37.8	13.3 (12 h)
Scrophulariaceae	*Castilleja communis*	7	green (flag red)	H–U	11–27, 18.8	1·5 (24 h)
Rubiaceae	*Hamelia patens*[5]	18	orange	H–P	11–20, 14.8	7·9 (24 h)
	Manettia aff. *sabiceoides*[5]	11	white	H	25–26, 25.5	3·9 (24 h)
Bromeliaceae	*Guzmania* sp.	15	purple & red	H–U	14–19, 17.8	11·9 (18 h)
Musaceae	*Musa* sp.	35	green	H–U	9–16, 13.0	84 (18 h)
Strelitziaceae	*Heliconia* sp.	30	yellow & red	H	—	—
Cannaceae	*Canna indica*	25	red	H–U	6–11, 7.3	29 (24 h)

Notes: [1] H = horizontal; P = pendent; U = upright.
[2] range and mean.
[3] means for day (24 h) or part of day.
[4] collection no. 49 (I.C.N. Herbarium); distinct from *C. pubescens* at Carare (Table 4).
[5] also visited by insects (*Ipomoea* and *Manettia* by Hymenoptera; *Mandevilla* and *Manettia* by Lepidoptera; *Eugenia* by various insects).

partially so (all except *Castilleja*). *Castilleja communis* differs from the others in having hidden closed green flowers beneath a rosette of red leaves.

Of these five native species, which are probably hummingbird-pollinated, only *Psammisia* cf. *penduliflora* was seen to have its corolla slit by nectar-thieving Bananaquits *Coereba flaveola,* which at Togui took the place of the flower-piercers (*Diglossa* spp.). There was evidence that such plundering was reduced by hummingbird territoriality. Thus 43% of the 28 flowers examined were slit in two small separate groups of 16 and 22 flowers, which were not defended by a hummingbird; but in a large plant with c. 300 flowers within the territory of an *Amazilia tzacatl,* none of 22 flowers examined were slit in this way.

Table 7 - Hummingbird feeding records, Togui

	P.g.	*A.n.*	*A.f.*	*A.c.*	*A.t.*	*C.g.*
Herbaceous plants, ground						
Castilleja communis						1
Musa sp. (banana)	6	17	11		1[1]	
Heliconia sp.	1					
Canna indica	2		9		1[1]	
Herbaceous plants, epiphytic						
Guzmania sp.				5		
Climbers						
Psammisia penduliflora			2		5	
Mandevilla aff. *mollissima*						2
Ipomoea sp.					2	3
Manettia aff. *sabiceoides*						10
Shrubs						
Cavendishia pubescens			6		7	
Hamelia patens			3	1	4	14
Trees						
Calliandra purdiei					5	
Eugenia jambos		9	27	38	67	
Insect-hawking		19	23	20	34	
Insect-gleaning	1	2		1	9	
Totals (368)	10	47	81	65	135	30

Hummingbirds abbreviated as follows: *A.c., Amazilia cyanifrons; A.f., Amazilia franciae; A.n., Anthracothorax nigricollis; A.t., Amazilia tzacatl; C.g. Chlorostilbon gibsoni; P.g., Phaethornis guy.*

Note: [1] nectar taken 'illegitimately', through pierce holes.

Feeding ecology of the hummingbirds

Six hummingbird species were resident on the hacienda at the time of our visit (Table 7), of which four *(A. tzacatl, A. cyanifrons, C. gibsoni, P. guy)* were seen nest-building. Two other species *(A. melanogenys, A. mulsant)* were each seen once. In spite of the degradation of the indigenous flora and the predominance of introduced plants, the six resident hummingbirds largely occupied different feeding niches.

The three *Amazilias* consisted of two territorial species *(A. tzacatl, A. cyanifrons)* and a non-territorial trap-liner *(A. franciae).* The main difference in their feeding ecologies is in

accordance with their relative bill-lengths, as measured by the bill/wing index (for further discussion see p. 136). In weight and wing-length the three species are similar (Table 1), but *franciae* has a considerably longer bill (bill/wing 45%, cf. 33% in *cyanifrons* and 37% in *tzacatl*). *A. franciae* fed at all levels, from herbaceous plants at 0·5 m to the tree canopy. At *Eugenia* trees it was dominated by the two other *Amazilia* spp., and consequently fed frequently at small, undefended trees with few flowers. The greatest amount of overlap was found in the feeding niches of *A. tzacatl* and *A. cyanifrons,* both of which held feeding territories at *Eugenia* trees. *A. cyanifrons,* however, tended to keep to higher levels and exploited a more limited range of plant species.

Anthracothorax nigricollis was territorial over high insect-hawking perches; a considerably larger bird than the *Amazilias,* it was able to feed unmolested at the ubiquitous *Eugenia* but did not defend its nectar. *Phaethornis guy* was a trap-line feeder on herbaceous plants with long corollas. *Chlorostilbon gibsoni* was also a trap-liner, feeding at low-growing flowers of herbs, shrubs and vines with short corollas, most of its nectar being shared with insects.

Amazilia tzacatl

A. tzacatl was probably the most abundant hummingbird on the hacienda. Single birds were observed feeding in 16 well separated areas, all except one of which were centred on *Eugenia* trees. The exception, which was not occupied until near the end of our visit, was centred on a climber, *Psammisia* cf. *penduliflora,* which had just come into flower. Conspecifics, *A. franciae,* and Bananaquits were chased from these territories. Although most feeding records were from *Eugenia, tzacatl* fed on a greater variety of flowers than any other hummingbird, from as low as 0·5 m to tree tops at 15 m. It was only once seen attempting to feed on banana flowers, when it went to a pierce hole probably made by a Bananaquit.

When feeding at *Eugenia, tzacatl* frequently (62% of records) uttered a monosyllabic *chack* between probes, but at small *Eugenias* with few flowers and after 1630 h such calling was rare. At two heaths over which *tzacatl* held feeding territories, *Psammisia* on the hacienda and *Cavendishia* about 6 km away, it also regularly called between feeding probes.

Frequently it gleaned insects from low, thick vegetation, at heights of 0·3 to 3 m (mean 1·9 m), e.g. from moss and the backs of leaves inside thick hedges and bushes, and along the underside of the midribs of banana leaves. It hawked also close to or inside thick vegetation, mainly (27 observations) from perches 4 to 11 m high, less often (6 observations) low over herbaceous vegetation from perches 1–2 m high. Hawking sallies were usually within 1·5 m of the perch and were directed at groups of flying insects, the bird often darting about and catching more than one insect per sally.

Amazilia cyanifrons

Single birds were observed feeding in 12 well separated areas on the hacienda, in nine of which the occupier regularly sang. All were centred on *Eugenia* trees. When taking nectar in these territories *cyanifrons* frequently uttered a monosyllabic *sip,* or *sick,* between probes. Unlike *tzacatl,* it visited *Eugenia* trees standing alone in pastures or along fences, 54% of *Eugenia* feeding records being at such trees. Except for one record at *Hamelia, cyanifrons* was not seen to descend from tree canopy level for nectar foraging. During 2 h watching at several *Cavendishia pubescens* bushes in a tree-shaded ravine 6 km from the hacienda, a *tzacatl* and two *franciae* frequently fed at the *Cavendishia,* but a *cyanifrons* remained in the trees above. Watches at the one flowering *Guzmania* plant, when it had 17 to 19 flowers in bloom, showed a *cyanifrons* silently visiting all flowers at each visit and returning to feed between 15 and 27 min later.

From its *Eugenia* territories *cyanifrons* displaced *franciae* and attempted, often unsuccess-fully, to displace Bananaquits. At a territory that overlapped the feeding area of a male *Anthracothorax nigricollis,* the visits of the latter were not disputed. The encounters which presumably established the division of the *Eugenia* trees between *tzacatl* and *cyanifrons* were not witnessed; where the two species had adjoining territories, the occasional silent

incursions of one bird into the territory of the other always coincided with the temporary absence of the owner. The choice of *Eugenia* territories by these two *Amazilia* was probably related to their insect-foraging methods, those of *tzacatl* requiring thicker vegetation at canopy, shrub and herbaceous levels while *cyanifrons* foraged for insects in more open places.

Between one and two hours after dawn, boundary encounters occurred between two, three and occasionally four *cyanifrons,* which sang from bare twigs 3–5 m up in an open area and also hawked for insects from the same perches. The insect-hawking recorded during the rest of the day was largely from higher perches (average of 12 records, 8·0 m), nine of them from trees with sparse foliage standing alone in pastures. Hawking sallies were either out from the crown or between the twigs and branches of the crown. There was only one record of *cyanifrons* gleaning for insects.

Amazilia franciae

This was the least abundant *Amazilia* on the hacienda. Only one singing male was located, whose territory, in a coffee and banana patch, a second male attempted to take over. Other males and females were recorded nectar-feeding along the tree-lined river banks and in a second coffee and banana patch. Except for *Eugenia,* the flowers that *franciae* visited had tubular corollas from 15 to 35 mm in length, on average longer than those visited by *tzacatl* (15–19 mm) and *cyanifrons* (15–18 mm). No defence of a feeding territory was observed; all nectar-feeding was silent, in contrast to the territorial *tzacatl* and *cyanifrons,* which frequently called between probes.

Most feeding records were from a male which was trapped and marked with a red dye, and was watched (both before and after being trapped) for a total of 18 h. This bird did much insect-hawking (28% of feeding records). Most sallies were short, about 30–60 cm from the perch, a single insect being captured. Perches used for hawking ranged from 1 to 5 m above ground level (average of 23, 2·5 m), and insects were usually caught close to vegetation, sometimes between the twigs of shrubs or the branches of low trees. Beside insect-catching, this male took nectar from *Canna, Hamelia, Eugenia* and banana flowers within the coffee patch, and also crossed 55 m of rough pasture to visit some *Eugenia* trees which were divided between adjacent territories of a *tzacatl* and a *cyanifrons.* Both of the territory-holders were seen to drive off the *franciae.*

Before 5 August the marked male *franciae* was heard to sing only once in 6 h of observation. Over a 4-day period, 5–8 August, another male *franciae* contested the possession of the territory with the owner. The encounters occurred almost entirely within an area measuring 26 × 14 m and at heights of 2–5 m. During this period, and for some days after the intruder had been ousted, the song output of the marked male was very high, averaging 44 song phrases an hour during the first 3 hours of the day. The intruder also occasionally sang while he was contesting possession. It seemed that the marked male's territorial behaviour was not defence of an insect-foraging area, because a *tzacatl* occasionally hawked for insects unmolested within 2–3 m of where he was perched. Presumably he was defending a potential mating site.

Anthracothorax nigricollis

This species was scarce at the time of our visit. In the first half of the period only a single territorial male was located on the finca; in the second half two more males were present and one or two females.

The first located male was watched for a total of 18 h. It occupied a territory measuring c. 55 × 15 m, containing shade trees 10–13 m tall, old citrus trees, banana plants and a rich herbaceous undergrowth. The territory overlapped the territories of a male *Amazilia franciae* and two *A. cyanifrons.* This bird fed largely by making frequent hawking sallies from exposed perches, often from the highest perch in the territory (13 m) or in the early morning and late evening from lower perches (mean height 10·2 m). In a typical sally it would fly 2–4 m out from the tree and make a number of darts from side to side before returning to its

perch. Its territorial activities were almost entirely directed to the protection of the airspace where it hawked. Except for one instance, when it displaced a *Phaethornis guy* from banana flowers, it was not seen contesting nectar sources. All three species of *Amazilia* came to feed at an *Eugenia* about 9 m from its main hawking perch but were not chased off; once it fed at *Eugenia* flowers within 1·5 m of the male *franciae* without any interaction. The male *A. franciae* whose territory overlapped that of the male *nigricollis* also frequently hawked for insects, from perches 1·5 m high, without interference; but on three occasions when it perched about 6 m up on the top of a half-dead citrus tree it was at once chased from the perch by the male *nigricollis*. It was ignored on one of its main perches 4·3 m up in the same tree. On eight occasions the male *nigricollis* chased off conspecific males which perched in his territory or flew over it.

A. *nigricollis* was seen to visit only two plants for nectar, both introduced (*Eugenia* and banana). Seven intervals between successive visits to the same banana flowers ranged from 19 to 55 min (mean, 37 min). Females were not recorded nectar-feeding, but on two occasions were seen gleaning for insects in thick hedges.

A. *nigricollis* was one of the nine species of hummingbirds whose feeding habits were studied at tropical levels in Trinidad (Snow & Snow, 1972). Insect-foraging, almost entirely by hawking from high perches, accounted for 38% of the Trinidad records, compared with 45% of all records at Togui. In both places this species fed more on insects than any other resident species of hummingbird.

Chlorostilbon gibsoni

C. *gibsoni* was the smallest hummingbird species regularly present on the hacienda. All but one of the feeding records were of female-plumaged birds, as were the two birds trapped. It was recorded nectar-feeding low down (0·3–4 m, mean, 1·8 m) in open unshaded pastures and along hedges. It was silent when feeding and did not appear to be territorial.

Of the five plant species visited, *Ipomoea* and *Manettia* were also visited by bees and their concentrated nectar (Table 6) is typical of bee-pollinated flowers. Three morning watches (0605–0805, 0700–0930 and 0935–1035 h) on a hedge where *Manettia* (15–20 flowers blooming) and *Hamelia* (45 flowers blooming) grew side by side, provided evidence that C. *gibsoni* stopped visiting *Manettia* when bees started feeding at it, between 0720 and 0755 h. In all *gibsoni* made 14 visits, returning at intervals ranging from 14 to 34 min (mean, 23 min). On the 8 visits up until 0800 h it visited both plants on 7 occasions and the *Manettia* only on one occasion; on the 6 visits after 0800 h only the *Hamelia* was visited, except at 0816 when the *Hamelia* and one bloom only of the *Manettia* were visited. Bees were not seen to feed at *Hamelia* but very occasionally butterflies did so. Timed feedings showed that C. *gibsoni* was able to exploit *Manettia* flowers more rapidly than *Hamelia* flowers; the time spent probing a flower (about 0·4 s) was almost the same for both plants, but as less time was taken in manoeuvring between *Manettia* flowers the rate of visiting them (one flower per 0·7 s) was higher than the rate for *Hamelia* flowers (one per 1·0 s). During these observations *Amazilia tzacatl* was often in view foraging for insects, and fed at *Hamelia* and at *Ipomoea* growing near by in the same hedge, but made no visit to *Manettia*.

Phaethornis guy

There were extremely few of this species on the hacienda, apparently only one or two females, and the two plants at which they were recorded feeding *(Musa* and *Canna)* were both introduced. A clump of *Heliconia* sp. in a ravine 5 km from Togui was also fed at by *P. guy*. These three herbaceous plants all have long (25–35 mm) curved tubular corollas, matching the bird's long curved bill. The two nests found were on banana leaves and no other plants with suitable leaves were seen on the hacienda. *P. guy* is essentially a forest hummingbird, specialized both in its feeding and in its nest-site (Snow, 1974). Its survival in this intensively farmed area is heavily dependent on the banana, which is planted to provide shade in young coffee plantations, and may be retained or cleared away after the main shade trees have grown.

Discussion

Faegri & Pijl (1966) list a number of morphological features of flowers that characterize the 'syndrome of ornithophily'. Stiles (1979) has extended them to include the phenology, nectar production, spacing on the plant, and other features of floral biology that may impinge on a plant's avian pollinators and thus be subject to coevolutionary selection. On the bird's side, a complex of characters, structural, physiological and behavioural, are related to nectar feeding and are presumed to have evolved in the course of development of the mutual relationship between bird and flower. An extensive and specialized literature has resulted from recent research into nectarivory in birds, with hummingbirds the main subjects. Emphasis has been especially on energetic aspects of the interaction, and the different feeding strategies that have resulted therefrom. It would be inappropriate to attempt here a thorough review of a fast-growing subject, and we confine the discussion to those aspects of the subject on which our observations provide new data or suggest modification of previous opinions.

The syndrome of ornithophily

Faegri & Pijl considered that the toughness that is characteristic of bird flowers is a protective adaptation against damage by the beaks of their avian pollinators, and this opinion seems to have been generally accepted. So far as hummingbird flowers are concerned, however, we think that the protective layers at the base of the flower are generally an adaptation protecting the nectar from nectar thieves and making it available only to legitimate visitors. The hard woody calyx of the pendent flowers of *Huilaea* (p. 119), very different from the rather delicate, insect-pollinated flowers of other melastomes, is a good example. Within the Ericaceae, the flowers of *Cavendishia pubescens* seemed to be effectively protected against nectar thieves by the bracts round the base (p. 120). There seems to be no good evidence that the delicate and exact probing of the bill of a hovering hummingbird damages even soft-tissued flowers.

Protection of a flower's nectar against thieves need not be absolute in order to be effective. At Fonté we had only a single record of the flower-piercer *Diglossa albilatera* piercing the flowers of *Cavendishia cordifolia*, which was very common in places where the flower-piercer was also abundant. The flower of *C. cordifolia* is moderately protected at its base, but is not immune to exploitation by *D. albilatera* (p. 120). It seemed likely that this flower-piercer was generally avoiding *Cavendishia* flowers at Fonté because they could exploit much more efficiently the unprotected flowers of another abundant plant, *Palicourea angustifolia*.

The orientation of the corolla tube is often a good indicator of the degree to which the flower is adapted for hummingbird pollination. This is well illustrated by the three species of *Palicourea* at Carare: in *P.* cf. *vagans*, the least specialized (corolla 9 mm, white; calyx yellow), the corolla tube is horizontal; in *P.* sp. 43 (corolla 15 mm, yellow; calyx red) between horizontal and pendent; and in *P. demissa*, the most specialized (corolla 31 mm, purple), pendent. Similarly *Huilaea* differs from other melastomes in having pendent flowers, and the specialized tree-heaths, e.g. *Psammisia falcata* and *Thibaudia rigidiflora*, from the unspecialized *Disterigma* sp. (Table 4).

The sugar concentration of the nectar, another important aspect of the syndrome of ornithophily, is discussed later in a separate section.

Specialized coevolutionary relationships

Just as a flower may be specialized to a greater or lesser degree for pollination by particular kinds of hummingbirds, so different hummingbird species are specialized to varying degrees for feeding at particular kinds of flower. As the most advanced mutual specialization one might imagine a flower adapted for pollination by only one species of hummingbird, which in turn might be dependent on the nectar of that one kind of flower. In fact it seems that, while very specialized flowers may indeed depend on a single hummingbird pollinator, even the most specialized hummingbirds usually feed from a number of different kinds of flower.

The most striking of the coevolutionary adaptations involving the hummingbirds that we observed is that between *Ensifera* and *Passiflora mixta.* Other species of *Passiflora,* e.g. *P. vitifolia* (Skutch, 1964) and *P. longiracemosa* (Snow, 1973), have flowers with long tubular corollas that are fed at, and probably pollinated, by long-billed hummingbirds, but the present case represents the extreme. It can hardly be doubted that the flowers of *P. mixta* evolved to their present length in step with the bill of *Ensifera.* The range of *P. mixta,* which has its centre of abundance at temperate levels in the Andes of Colombia and Ecuador, corresponds broadly with the range of *Ensifera* (Andes of north-western Venezuela south through Colombia, Ecuador and Peru to northern Bolivia); but *P. mixta* now occurs also in a few scattered localities in the coastal range of northern Venezuela beyond the range of *Ensifera.* This is, however, almost certainly due to introduction by Amerindians, who have long made use of *P. mixta*'s highly edible fruit (S. Tillett, pers. comm.).

We recorded *Ensifera* feeding at no other kind of flower; indeed there were no plants in flower at the time of our visit approaching *Passiflora mixta* in length of corolla. *Ensifera* is, however, generally said to be adapted to feeding at *Datura* flowers. It certainly feeds at *Datura* flowers, but it may be doubted whether this is a case of coevolutionary adaptation. *Datura* flowers have few ornithophilous features; they are widely open at the mouth, so that shorter-billed hummingbirds than *Ensifera* can feed at them by getting their heads well inside the corolla tube (pers. obs.), the anthers and stigma are not exserted so as to come into contact with *Ensifera*'s forehead (as they are in *P. mixta*), and the corolla is thin-walled and easily pierced. We saw no *Datura* growing wild in the area where we worked, but they were common ornamental plants round houses. *Datura* is a small genus of only 10 species, occurring in tropical America but widespread elsewhere in tropical and warm temperature areas. Its pollination has not been thoroughly studied. *D. meteloides* is visited by a hawk moth which enters the corolla tube (Baker, 1961), and the open vase shape of the flowers suggests that they are adapted to facilitate the bodily entry of pollinators rather than to restrict their nectar to pollinators with very long bills or probosces. The white colour of most *Datura* flowers suggests adaptation to a crepuscular pollinator. Two species have red flowers, a colour typical of hummingbird flowers but also found in some moth-pollinated flowers (Baker, *loc. cit.*). We provisionally conclude that *Ensifera* is adapted primarily to *Passiflora mixta* and other species of *Passiflora* with very long corolla tubes, and that its habit of feeding at *Datura* flowers is a result of man's alteration of its habitat. But it would be desirable to study *Ensifera*'s feeding habits in an area, if there be any, where a red-flowered *Datura* grows wild.

Also needing further study is the effect of exploitation of the nectar of *Passiflora mixta* by flower-piercers and the hummingbirds that make use of the holes made by flower-piercers. In the Fonté study area nectar-thieving reduced the amount of nectar available to *Ensifera* to such an extent that it must surely have affected *Ensifera*'s abundance. Yet there is every reason to suppose that these or similar nectar thieves have been present for as long as *Ensifera* and *P. mixta* have existed. Our experimental protection of *Passiflora* flowers showed that *Ensifera* could obtain all the nectar that it could ingest from one or two flowers of the dozen or so available on a plant. Had the experiments continued, it would have been of great interest to have seen whether individual *Ensiferas* would have switched from trap-lining, over what must have been considerable distances, to territoriality at single *Passiflora* clumps. The effect of territoriality, from the plant's point of view, would be greatly to increase the incidence of self-pollination. Trap-lining by *Ensifera,* on the other hand, must promote out-crossing (Linhart, 1973). Hence it might be advantageous for the plant not to evolve increased protection of the nectar from nectar thieves, but to maintain its pollinator at low population densities; but such a course would be hazardous, since it would carry the risk of occasional local disappearance of the pollinator.

Lafresnaya, the only temperate-level Andean hummingbird with a long curved bill, was recorded feeding mainly at three kinds of flowers with long, curved corolla tubes that fitted its bill closely *(Pentadenia strigosa, Castilleja fissifolia, Siphocampylus bogotensis).* None of these flowers was seen to be fed at 'legitimately' by any other hummingbird species. It is

reasonable to conclude that *Lafresnaya* is the main pollinator of these three plants, and that their flower structure coevolved with *Lafresnaya*'s bill. The situation is not simple, however: *Lafresnaya* males and females have distinctly different bill-lengths, that of the male being shorter although the male's wing is longer than the female's. This sex difference suggests that the male is likely to be more territorial than the female, and also to be less specialized in its feeding habits (see next section). Our limited observations did in fact suggest that *Lafresnaya* females were trap-liners and that some, at least, of the males held feeding territories.

The only other specialized coadaptations between particular hummingbird species and flowers suggested by our observations were those between the three hummingbirds with long straight bills at Carare, *Coeligena prunellei*, *C. torquata* and *Doryfera ludoviciae,* and some of the flowers at which they fed. *C. prunellei* and *Doryfera* were the only two hummingbirds seen feeding legitimately on the heath *Psammisia falcata,* whose long corolla tube is filled with densely packed stamens, necessitating a considerable upward thrust by a hovering hummingbird in order to reach the nectar; and *C. torquata* (a smaller species, subordinate to *C. prunellei,* but with an even longer and markedly finer bill) appeared to be the only species capable of exploiting the specialized and very narrow-tubed flowers of *Bomarea* cf. *carderi.*

Trap-lining vs. territoriality

The broad distinction between trap-lining and territoriality as alternative foraging strategies for hummingbirds has been mentioned earlier. Feinsinger & Colwell (1978) have recently made a more refined classification, defining four community roles available to hummingbirds. They distinguish two kinds of trap-liners. 'High-reward' trap-liners are species with either particularly long or curved bills, which have coevolved with certain plant species that offer high nectar rewards per flower, the nectar being inaccessible to other hummingbirds. These are the species usually referred to as trap-liners. 'Low-reward' trap-liners are small, shorter-billed species, which are excluded from clumped flowers by territorialists and instead visit dispersed, unspecialized flowers. Hummingbirds in this second category are not found in all communities. Territorialists form a third category, and the fourth consists of 'territory-parasites', which may either be large birds with moderate-length beaks that can forage with impunity among flowers defended by smaller territorialists, or very small, short-billed species which can infiltrate into territories, often feeding in parts of the territory not much used by the owners. In addition to beak characteristics and body size, wing-disc loading has been shown to be important in fitting a hummingbird for a particular foraging strategy (Feinsinger & Chaplin, 1975). Species with high wing-disc loading (high weight in relation to wing-length) are more manoeuvrable, have greater acceleration, but are less efficient at hovering than species with low wing-disc loading. The former tend to be territorialists (being better in aggressive encounters and having less need for sustained flight), and the latter trap-liners.

The hummingbirds in our study areas fitted into Feinsinger & Colwell's four categories well; but on the basis of available weights and measurements there is no clear relationship between foraging strategies and wing-disc loading. Thus *Ensifera,* the most pronounced trap-liner, has the highest wing-disc loading (·0489) and *Metallura,* a territorialist, the lowest (·0257). *Coeligena torquata,* a typical trap-liner, and *C. prunellei,* a more territorial species, both have wing-disc loadings of ·0281. It is likely that the lack of relationship is due in part to the small samples of weights available to us, some of which are from other areas. We draw attention instead to the ratio between bill-length and wing-length, given as a percentage in Table 1. This proves to be a good indicator of feeding strategy, and has the advantage that it can be consistently derived from museum specimens.

There were 10 species with bill/wing percentages of 38 or over (Table 1), all but two of which were high-reward trap-liners. The two with the highest percentages (*Ensifera* and *Phaethornis guy*) show the highest degree of feeding specialization. The exceptions were *Acestrura mulsant,* which although apparently a trap-liner was not seen to visit any flowers to which it had exclusive or nearly exclusive access. Observations were, however, few. The

other exception, *Chlorostilbon poortmani,* was a low-reward trap-liner which exploited the less specialized hummingbird flowers and some bee-pollinated flowers.

Eight of the 12 hummingbirds with bill/wing percentages between 20 and 32 were territorial over high-density, morphologically less specialized ornithophilous flowers (e.g. *Guzmania cryptanta, Palicourea* sp. 43) or over high-density flowers also available to insects (e.g. *Clusia, Eugenia*). They also frequently hawked for insects. Three forest species (*Adelomyia, Ocreatus, Aglaiocercus*), however, were not seen to be territorial. Excluding pierce-hole feeding, 80% of nectar-feeding records for these three species were at flowers also visited by insects, mostly large bees. Some large bees are trap-line feeders at dispersed specialized flowers, and possibly these hummingbirds are adapted in some way to share this nectar source. There were insufficient observations to determine the feeding strategy of *Colibri thalassinus,* but in Costa Rica Wolf *et al.* (1976) found that it defended a specialized hummingbird flower, mostly from conspecifics.

The three *Amazilias* at Togui, the only three congeneric species resident in the same locality, have bill/wing percentages closely related to their observed feeding strategies: *A. franciae,* a trap-liner – 45·2; *A. cyanifrons,* almost entirely territorial over one concentrated nectar source (*Eugenia*) – 32·6; and *A. tzacatl,* territorial over the same nectar source, also over hummingbird flowers with moderate-length corollas, and in addition exploiting a variety of more dispersed plants – 37·1. The two *Coeligena* species at Carare showed slight niche differences which can be related to bill/wing percentages, *prunellei* (38·3) showing some territorial tendencies and *torquata* (40·8) being a trap-liner with possibly exclusive access to one plant species.

Nectar characteristics

The sugar concentration of the nectar of many hummingbird-pollinated flowers is relatively low, averaging about 20% (weight/total weight of solution) (Baker, 1975). Bee-pollinated flowers have more concentrated nectar. The greater dilution of hummingbird nectar is at first sight puzzling, since it has been shown experimentally that, given a choice, hummingbirds prefer the most concentrated solution (Hainsworth & Wolf, 1976). Bolten & Feinsinger (1978) have argued that the dilute nectar typical of hummingbird flowers may have evolved to deter bees, which need more concentrated nectar, and that once a flower has evolved adaptations to exclude bees, selective pressure from feeding hummingbirds may lead to a return to more concentrated nectar. They present evidence from Trinidad in support of this hypothesis.

The flowers whose nectar concentrations are given in Tables 2, 4 and 6 can be divided into three groups: flowers visited by bees as well as hummingbirds (*Aphelandra, Disterigma, Ipomoea, Manettia, Palicourea* cf. *vagans, Phaseolus*); the less specialized hummingbird flowers, with corolla lengths of 11–20 mm (10 species); and the more specialized hummingbird flowers, with corolla lengths of 21–114 mm (9 species). The ranges and means of nectar concentrations for these groups were, respectively, 23–38, mean 29·2%; 14–21, mean 16·8%; and 14–27, mean 19·5%. These figures are in good agreement with Bolten & Feinsinger's hypothesis. It may be noted that two of the morphologically most specialized species, *Passiflora mixta* (25·5%) and *Pentadenia strigosa* (27·0%), had the highest concentrations among the hummingbird flowers.

Ornithophily in the Andean flora

Our data are far too incomplete for any survey of the incidence of ornithophily among Andean plants, and the literature on the subject is very limited; but a few points deserve mention.

It seems clear that three plant families, the Rubiaceae, Ericaceae and Bromeliaceae, are of prime importance, the first mainly for short-billed, unspecialized hummingbirds, the second and third both for unspecialized and for some of the more specialized hummingbirds with long straight bills. In the richest of our three study areas these three families accounted for nearly two-thirds (14 out of 22) of the plant species providing nectar at the time of our visit;

in the two other areas, with poorer vegetation modified by agriculture, the proportions were lower (6 out of 15, and 4 out of 13). Members of the Rubiaceae and Ericaceae provide examples of different degrees of specialization for ornithophily, from such unspecialized flowers as *Palicourea* cf. *vagans* (Rubiaceae) and *Disterigma* spp. (Ericaceae), which have white flowers with short corolla tubes that were visited by insects as well as short-billed hummingbirds, to specialized flowers such as *Palicourea demissa* (Rubiaceae) and *Psammisia falcata* (Ericaceae), which were visited only by two long-billed species. The bromeliads as a family seem to be adapted for pollination by hummingbirds (McWilliams, 1974).

To what extent pollination by hummingbirds has affected speciation and interspecific differences in phenology within these families is a matter for future research. *Palicourea* is a large and taxonomically difficult genus, with about 200 known species (Willis, 1973). Specialization of the flower for pollination by different hummingbird species or groups of species may have led to divergence between taxa (in geographical isolation ?), resulting in reproductive isolation when they later became sympatric. Competition for pollinators between morphologically similar sympatric species may have led to the staggering of flowering seasons, as appears to have happened in Costa Rican *Heliconia* species (Stiles, 1975). It is noteworthy that bromeliads in particular tend to have very restricted flowering seasons, so that observations conducted over a short period give a very incomplete picture of their importance for hummingbirds. The four species that were in flower in our three study areas at the time of our visit were only a fraction of the species present.

The remaining hummingbird flowers belonged to 18 different families (omitting introduced plants), with only one or two species in each. Most of these families are well known to contain ornithophilous genera, the most interesting of the exceptions being the Melastomataceae. This very large family, with numerous neotropical species, is typically insect-pollinated; the flowers are open or have only short corolla tubes. The genus *Huilaea,* with a single species, is known only from a few temperate forest localities in Colombia. Its flowers are strikingly different from typical melastome flowers, showing several ornithophilous features, and it is reasonable to suppose that it evolved in association with forest hummingbirds. Whether it is generally associated with *Boissoneaua flavescens,* which held territories at the *Huilaea* trees at Carare, must await further study.

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